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

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# Abstract

Accurately measuring tree carbon (C) allocation above and belowground remains a difficult task and is challenging to represent in models of forest C cycling. Understanding how global change impacts the distribution of tree photosynthetic C is an essential process in determining future terrestrial C balance. We utilized climate-controlled whole tree chambers (WTC) to measure aboveground net CO2 fluxes of*Eucalyptus tereticornis* trees, which were expected to correlate to harvested tree C mass. This study investigated how treatment manipulations of CO2 and drought affected both tree biomass partitioning and the allocation of photosynthetic C to various above and belowground pools. For each WTC, we calculated total belowground C allocation (TBCA) as the residual between the aboveground net CO2 flux and aboveground C mass. It was hypothesized that that both drought and elevated CO2 would increase both partitioning of biomass to roots and TBCA. The measured cumulative aboveground tree net CO2 flux correlated positively to both whole tree C mass and mean leaf area over the final 11 months of the experiment. Surprisingly, biomass partitioning to roots was not affected by elevated CO2 or drought. Instead, increases in biomass partitioning to leaves and decreases in aboveground wood were detected under elevated CO2. Total C allocation to leaves was increased under elevated CO2, while allocation to aboveground wood and TBCA were not affected by either treatment. Across, the final 11 months of the experiment the daily fraction of C uptake allocated belowground remained relatively constant, regardless of climate change treatment or tree size. Overall, we show that elevated CO2 affects biomass partitioning, beyond ontogeny, aboveground instead of belowground. In addition, the unique design of the WTC also provides evidence that elevated CO2 may not always enhance C allocation belowground, as has been previously shown. These results reveal how climate change factors can impact the investment of photosynthetic C in a Eucalyptus tree species and provide an empirical framework to improve model representations of tree C allocation.

## Key Words

carbon allocation, biomass partitioning, whole tree chambers, elevated CO2, drought

# 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 maximize 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).

Variation in C allocation responses to environmental change combined with a lack of understanding of the mechanisms driving C allocation impede accurate modelling of terrestrial C cycling (Friedlingstein et al. 1999, Landsberg 2003, Litton et al. 2007, Epron et al. 2012, McMurtrie and Dewar 2013). The representation of C allocation lags behind photosynthesis (A) in applied forest models (Friedlingstein et al. 1999, Franklin et al. 2012, Iversen and Norby 2014) and this deficiency is due to the difficulty in defining guiding principles that are valid under a wide range of conditions (Franklin et al. 2012, Mäkelä 2012). Partitioning coefficients or fixed fractions of assimilation to individual components are often used in process-based models of forest C cycling (Litton et al. 2007, Franklin et al. 2012). Unfortunately, using inappropriate or over simplified allocation schemes can lead to models producing unintended responses or giving the expected answer for the wrong reason (De Kauwe et al. 2014, Fatichi et al. 2014). 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.

This allocation of photosynthetic C above and belowground is an important factor in terrestrial C cycling yet our knowledge of how global change impacts C allocation 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 Poorter et al. (2000) concluded that on average allocation to stem, root, or leaf mass fractions did not change in plants grown under elevated Ca. Alternatively, the total flux of C belowground (TBCA), which includes all belowground processes, was enhanced under elevated Ca across four forested free-air Ca enrichment experiments (Palmroth et al. 2006). In forest ecosystems this enhancement can be attributed to factors such as increases in C allocation to roots biomass (Iversen 2010) or root exudation (Phillips et al. 2011).

The response of forest to global change also depends on teasing apart complex relationships between interacting factors (Rustad 2008). For example, drought stress in trees can have deleterious effects on leaf (Bradford and Hsiao 1982, Schulze et al. 1987, Broeckx et al. 2014), stem (Brando et al. 2008) and root production (Meier and Leuschner 2008, Anderegg 2012). It has also been shown that C allocation to root systems can increase in drought environments when the severity and duration of the drought periods are substantial (Poorter et al. 2012). The effects of drought may limit C sequestration by the terrestrial biosphere (Iversen and Norby 2014), yet how limitations imposed by drought interact with the growth-stimulating effects of increasing Ca requires more attention (Duursma et al. 2011).

Despite its importance, data on TBCA remain sparse and reliable estimates of root biomass, exudation, turnover and respiration in field conditions are difficult to obtain (Cheng et al. 2005, Litton et al. 2007, Phillips et al. 2008, Strand et al. 2008, 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 C allocation is often estimated as a residual, by subtracting the changes in C pools of litter, soil and roots from total 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 C pools are in steady-state conditions (Raich and Nadelhoffer 1989), which is not always the 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 C belowground.

The whole-tree chambers (WTC), located at the Hawkesbury Forest Experiment, were designed to allow continuous measurement of whole-tree net CO2 fluxes, allowing A and respiration 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 also controlling temperature and air humidity. Combining the high resolution CO2 flux measurements with an evergreen *Eucalpytus* species, that provides near constant annual production, enables tree C allocation to be tracked over long periods of time. This experimental system can then be used to validate models that scale leaf A 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 *Eucalyptus saligna* Sm. trees grown under elevated Ca were smaller than ambient trees and that larger trees had a smaller reduction in canopy transpiration in drought conditions, via deeper rooting access to water resources (Duursma et al. 2011). Therefore, the specific objectives of this study were to determine the response of biomass partitioning among foliage, aboveground woody components and roots of a native Australian tree species to changes in Ca and altered water availability. Utilizing the unique WTC design we aimed to test how cumulative net aboveground C gain correlates to whole tree C mass increment, as a function of tree size. We then applied a mass balance approach to track the allocation of C above and belowground across the final eleven months of the experiment.

(1) As C uptake and growth should be coordinated over long time periods, we expected both total leaf area and harvested tree C mass to correlate with cumulative total aboveground net canopy C uptake.

(2) At then end of the 2 year experiment we expected partitioning of C to roots to increase under elevated Ca, similar to previous studies. We also expected increases in partitioning to roots under drought treatments, as trees should attempt to reduce water limitation.

(3) As shifts in partitioning to root biomass were hypothesized, we expected TBCA to increase through time as cumulative tree C flux became affected by elevated Ca and drought. Additionally, we expected C allocation to leaves and woody tissue components aboveground to remain constant over the final eleven months of the experiment.

# Methods

## Terms

*Mass partitioning*: the relative distribution of biomass between different tree tissue components such as leaves, branches, boles and roots.  
*Carbon allocation*: the fraction of net primary productivity distributed to different ecosystem components such as specific tissue components or total belowground pools.

## Whole tree chamber experimental design

From April 2007 *Eucalyptus saligna* seedlings were grown in 12 WTC at the Hawkesbury Forest Experiment in Richmond, Australia. One seedling per WTC (9 m high) was grown for 2 years 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 grow freely below 1 m. Full descriptions of the chamber design and operation are provided in Barton et al. (2010). This multi-factor 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 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.

## Aboveground 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 from April 2008 to March 2009. 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. Cumulative daily net aboveground C fluxes (, g C d-1), representing daily gross aboveground primary productivity of each tree minus respiration of leaves, stems and branches, were summed () to compare to harvested tree C mass, leaf area and C allocation above and belowground.

## Harvested tree carbon mass

A final destructive harvest was completed in 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 sieving all soil inside each root exclusion barrier to the hard layer. Five roots cores (10 mm diameter), sampled before the harvest, 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 data (below). Leaf and litter C mass was calculated by multiplying biomass by the WTC specific mean leaf C content (%). Leaf C content was determined from a sub-sample 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 C mass by total C 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 allometry surveys

Tree height was measured bi-weekly and diameters were recorded monthly at regular intervals (30 cm) along the main bole and split stems. Bole diameters at 65 cm height were used as the reference diameter. Diameter and length for every branch, including forked branches, were surveyed seven times between April 2008 and March 2009. 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 recorded as described above and 1 cm sections were removed from the bole at regular intervals between diameter measurements. Wood density for each section was calculated by dividing the dry mass by the fresh volume separately for bark and wood. The mean total bole density for each tree (, g cm-3) was then calculated as the total density of bark and wood, weighted by the total diameter of each section. We assumed that did not change through time.

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 top section was calculated as a cone with a tip radius of .001 cm. The volume below the reference 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 (from tree top to 65 cm). This resulted in two additional stem sections with taper assumed as above. All bole volume units were then summed (including forked stems) to calculate total tree volume. Bole mass was calculated as total volume multiplied by WTC specific .

## Branch carbon

Measured dry mass, length and basal area of harvested branches was used to determine the branch density () as well as a geometric shape factor (, see Mäkelä 1997) for each WTC by rearranging the equation:

(1)

where is summed dry mass of all harvested branches, is total branch length (cm), is total branch basal area (cm3), represents the combined density of wood and bark (g cm-3) and corrects branch volume estimates to an intermediate shape between a cone and a cylinder. The ratio of measured to was used to generate a WTC-specific .

During each survey period, Mbr was estimated by solving the above equation with and for individual branches with specific to each WTC. 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. We assumed that did not change through time. Total dry branch mass at each survey point was the total mass of all individual branches.

## 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, between April 2008 and March 2009, 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:

(2)

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:

(3)

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.

## Tissue C allocation

Tissue specific C allocation represents the fraction of net primary productivity (NPP) distributed to a given tissue, which determines the change in biomass of that tissue through time such that:

(4)

where is the standing C mass of a component (g C), is the allocation to that component (0-1) and is the component specific turnover (d-1).

Here, total C allocation to leaves and aboveground wood (branches + stems) could be estimated from the sums of tissue C mass, net aboveground C flux and tissue turnover for each day of the experiment such that:

(5)

where is the total dry C mass of either component and is the daily net aboveground C flux (g C d-1). For example, C allocation () to leaves was determined by combining measurements of harvested dry C mass of leaves () with and total cumulative litterfall () such that:

(6)

and then solving for leaf C allocation:

(7)

Allocation to aboveground wood C was estimated in the same manner with turnover measured as total dry C mass of branch litter collected across the experiment. As root turnover was not measured only total belowground C allocation (TBCA) could be calculated (explained below).

## Total belowground carbon allocation

As the installation of chamber floors into each WTC separated the aboveground CO2 uptake from the soil CO2 efflux, TBCA at any time point was calculated as:

(8)

where is the gross primary productivity (g C) of each tree aboveground minus respiration of leaves, stems and branches and is the aboveground standing crop C 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 C mass of roots () and the residual belowground C flux (). The residual belowground C flux includes; root and soil respiration, root turnover, root exudation and any unaccounted for root C 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 eleven months of the experiment while was calculated at the final harvest.

## Mass balance relationships between and carbon allocation.

The cumulative sum of , at any given time point, represented the net C uptake for each WTC. Daily allocation of C to boles and branches was estimated by linear interpolation between survey measurements and the final harvest, starting at the first branch survey (April 2008). Daily modeled estimates of leaf and litter C were added to bole and branch C mass to estimate on any given day. The contribution of each aboveground component to the cumulative sum of were then tracked from April 2008 to March 2009. The initial estimated C 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. This allowed daily estimates of TBCA to be generated across the final 11 months of the experiment. Additionally, the significant log-linear relationship between aboveground mass of both harvested trees and potted seedlings (R2 = 0.98) was used to predict on the last day from . At the end of the eleven month period, correlations between , whole tree C mass and leaf area with were tested.

## Data analysis

Differences in experimental parameters to the interaction of Ca and drought treatments at the final harvest were analysed using two-way ANOVA in R (R Development Core Team 2011). Tukey's post-hoc tests were performed in conjunction with ANOVA to determine which specific paired comparisons among climate change treatments were different. Results were considered significant at P ≤ 0.05.

# Results

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

Over the final year of the experiment, was significantly reduced by 30.5 % under eCa (P = 0.043), while no effects of the drought treatment were detected (Table 1). Similarly, both whole tree C and from the final harvest were reduced under eCa by ca. 32 % (both P < 0.03). was positively correlated with both whole tree C (R2 = 0.74, Figure 1,a) and (R2 = 0.69, Figure 1,b).

Leaf area at the final harvest was significantly reduced by by 31.3 % under eCa (p < 0.001), and this pattern was observed across the final eleven months of the experiment (Figure 2). Overall, was positively correlated with mean daily leaf area (P < 0.001, Figure 3).

## Tree carbon mass partitioning

Carbon mass partitioning to individual tissue components, at then end of the experiment, was affected differentially under eCa (Table 1). Aboveground woody C mass was (boles+branches) was reduced 37 % under eCa (P = 0.0151), driven mostly by eCa effects on boles. Neither leaf or litterfall C mass were affected by Ca and drought treatments. Total root C mass was marginally reduced under eCa (P = 0.091) but not affected by drought.

The C mass fractions of leaves, stems and roots, at then end of the experiment, were also affected differentially under eCa. Leaf mass fraction was increased by 15.2 % under eCa (P = 0.031) but was not affected by the drought treatment. Leaf mass fraction was negatively correlated with whole tree C (P= 0.004, Figure 4a). Stem mass fraction was reduced by 8 % under elevated CO2 (P = 0.014), with no effect of the drought treatment detected. Stem mass fraction was was positively correlated with whole tree C (P = 0.008, Figure 4c). Root mass fraction was not affected by either treatment and was not correlated to whole tree C (Figure 4e). Over the final eleven months of the experiment, leaf mass fraction was negatively correlated with (R2 = -0.54, P = 0.006). Neither SMF nor RMF were correlated with F[c,t] during this time period.

## Aboveground carbon allocation

At the end of the experiment, the total C allocation to leaves increased by 28 % under eCa (P = 0.037), with no effect of the drought treatment detected. Leaf C allocation was was negatively correlated with adjusted (P = 0.031, Figure 4b). Alternatively, C allocation to aboveground wood was not affected by either treatment and was not correlated to whole tree C (Figure 4d).

## Belowground carbon allocation

Within each treatment combination the cumulative C 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 TBCA and . Neither TBCA nor were affected by Ca or drought treatments (Figure 6). TBCA and adjusted were positively correlated over the final 11 months of the experiment (R2 = 0.78, P < 0.001) and the proportion of C allocated belowground was relatively constant through time and between treatments (Figure 7). TBCA was positively correlated with mean daily leaf area (R2 = 0.44, P = 0.019).

# Discussion

# List of Tables

**Table 1**. Final harvest C mass of above and belowground tissues and cumulative aboveground tree C flux. Each value represents the mean (± 1 standard error) for each treatment combination and units for all values are g C. For each component, different letters represent significant differences between treatments with the overall model which includes Ca \* Drought interactions. Each P value represent overall differences within individual components of the main treatment effects of the Ca or Drought and treatment interactions of eCa and Drought.

# List of Figures

**Figure 1**. Treatment means of harvested whole tree carbon mass (a) and aboveground carbon mass (b) as a function of cumulative aboveground C 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 C (R2 = 0.86) and aboveground C mass (R^2 = 0.78).

**Figure 2**. Estimated canopy leaf area for each WTC tree over the final eleven months of the experiment (April 2008 to March 2009). 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 aboveground C flux as a function on mean daily leaf area over the final eleven months of the experiment. The solid line represents the significant linear model fit (R2 = 0.77).

**Figure 4**. Treatment means of C mass fractions of leaves (a), stems (boles + branches) (c) and roots (e) at final harvest as a function of tree size, via total tree C mass. Treatment means of total C allocation to leaves (b) and stems (d) as a function of total aboveground net C flux. Root C allocation could not be estimated as root turnover was not known. Solid lines represent overall model fit for leaf, stem and root mass fractions (R2 = -0.57, 0.52 and 0.02, respectively), as well as leaf and stem C allocation (R2 = -0.39, 0.01, respectively).

**Figure 5**. Cumulative aboveground C flux and additive C allocation to individual tree components from 2008-4-15 to 2009-3-16. Each panel represents mean values for each treatment combination (n=3). Both C flux and tissue C allocation where set to 0 on 2008-4-15 in order to track the allocation of C in daily time steps. Total root C 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 total aboveground net C flux, total belowground c allocation, and the residual belowground C flux at the final harvest.

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

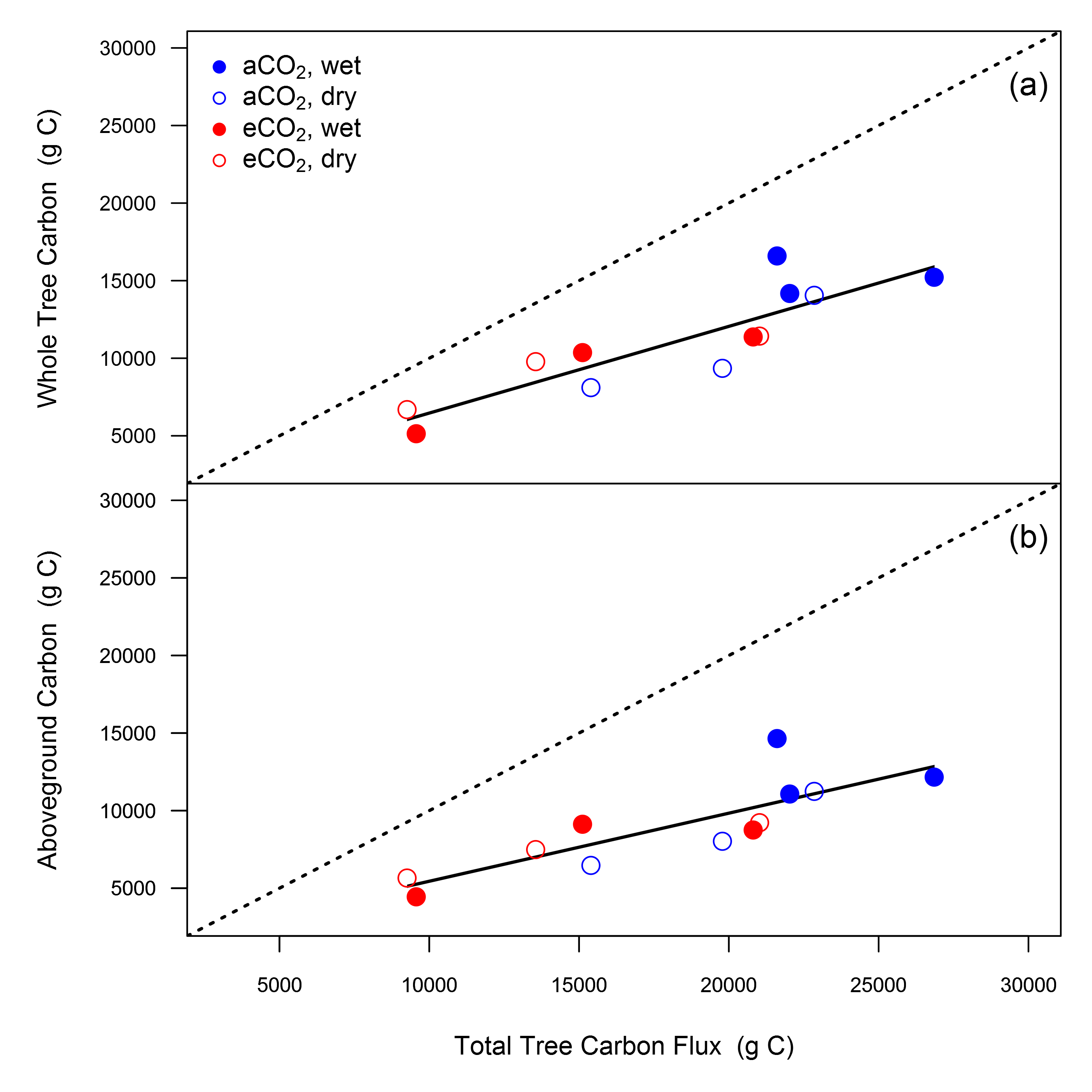
**Figure S1**. Cumulative aboveground C flux and additive C allocation of individual tree components from 2008-4-15 and 2009-3-16. Panels represent each individual WTC. Both C flux and tissue C allocation where set to 0 on 2008-4-15 in order to track the allocation of C in daily time steps. Total root C 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.

# Tables

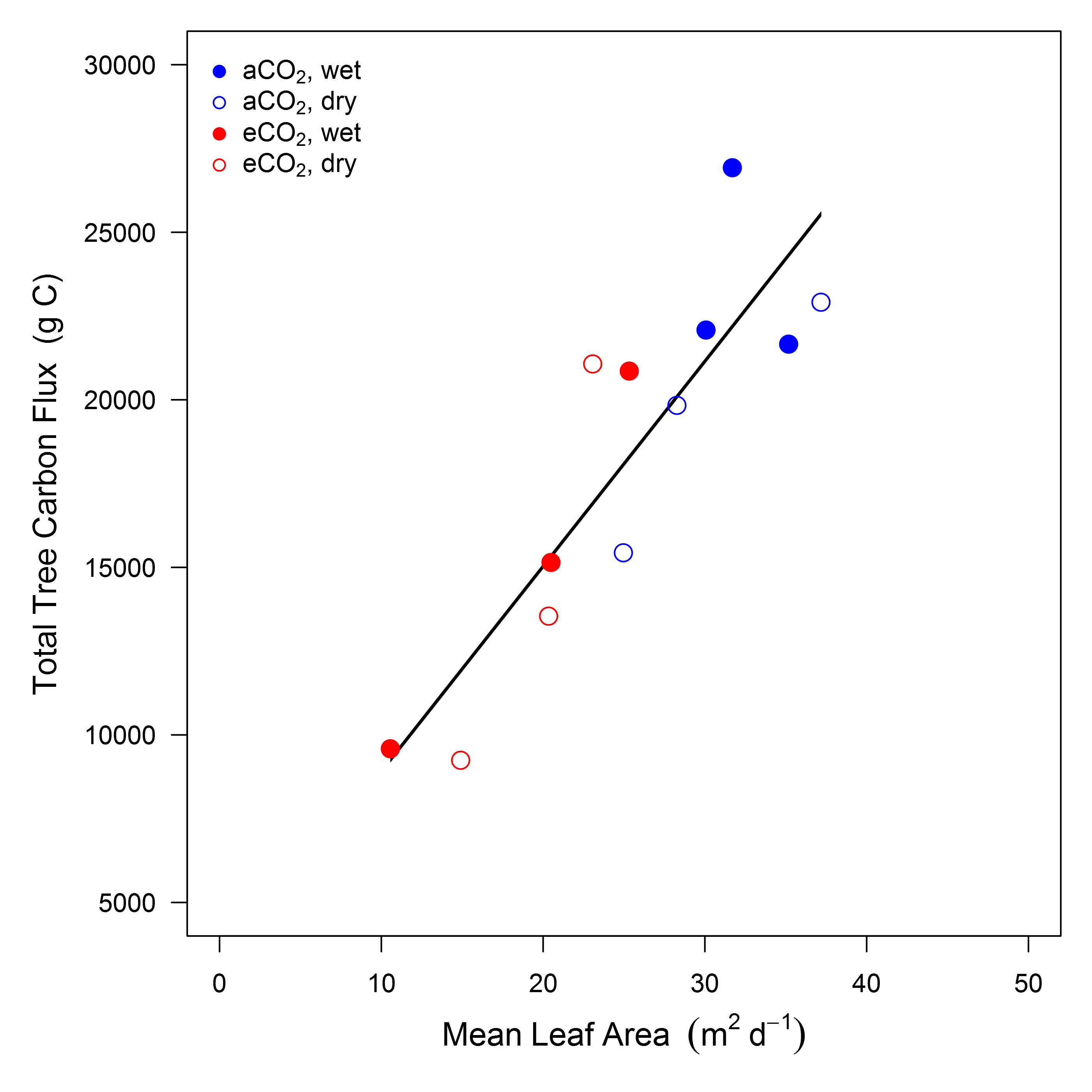
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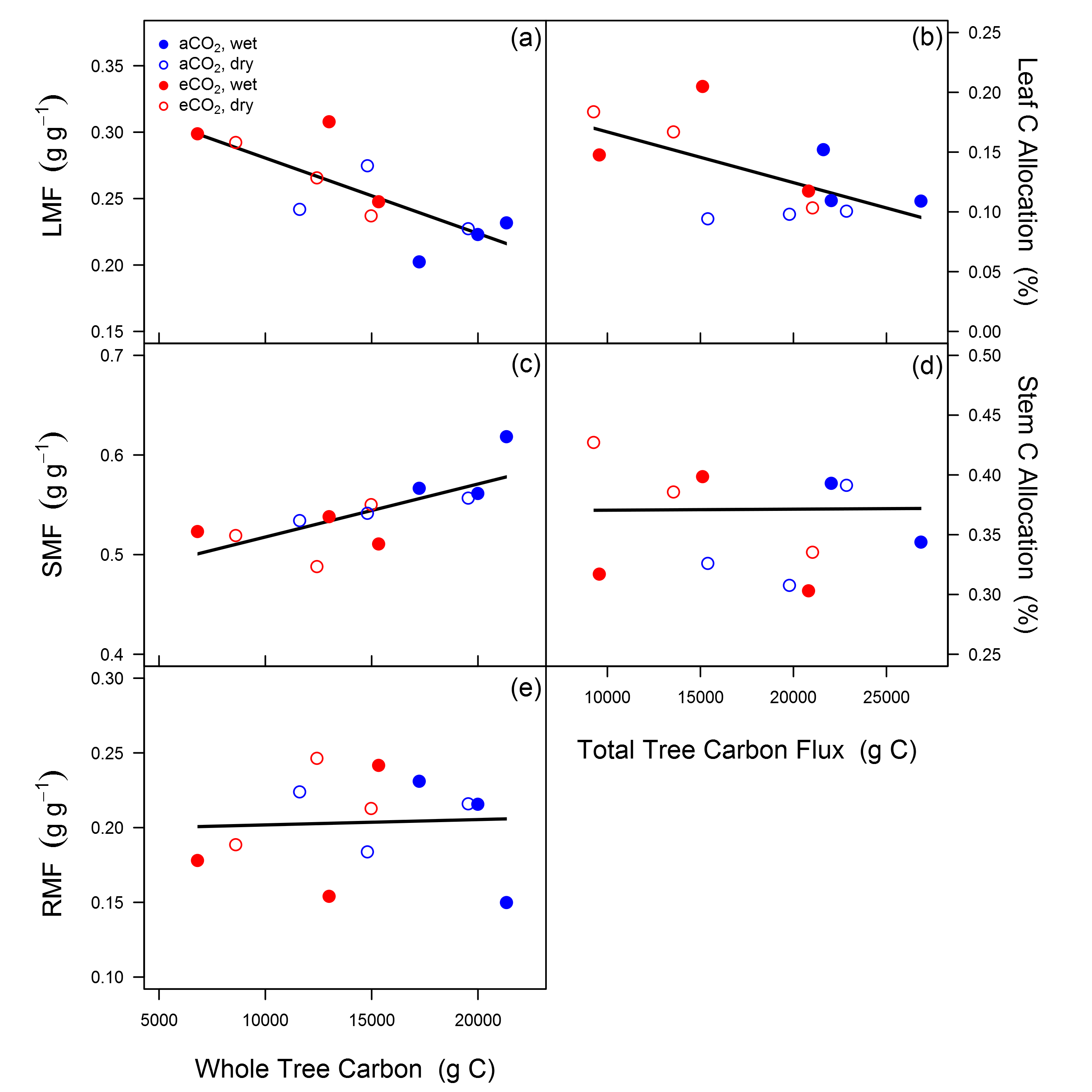
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| --- | --- | --- | --- | --- | --- | --- |
| **Treatment** | **Bole** | **Branch** | **Leaf** | **Litter** | **Root** | **Fc,T** |
| aCO2-dry | 5449.8 (715.6) b | 2915.9 (654.4) a | 2642.8 (370.7) a | 1129.8 (336.0) a | 3180.1 (521.0) a | 19394.2 (2169.5) a |
| aCO2-wet | 8109.4 (278.2) ab | 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-dry | 4250.6 (710.9) a | 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-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 |
| CO2 effect (P) | 0.005 | 0.086 | 0.122 | 0.417 | 0.091 | 0.044 |
| Drought effect (P) | 0.085 | 0.803 | 0.358 | 0.897 | 0.766 | 0.413 |
| CO2 \* Drought (P) | 0.075 | 0.712 | 0.539 | 0.792 | 0.397 | 0.532 |

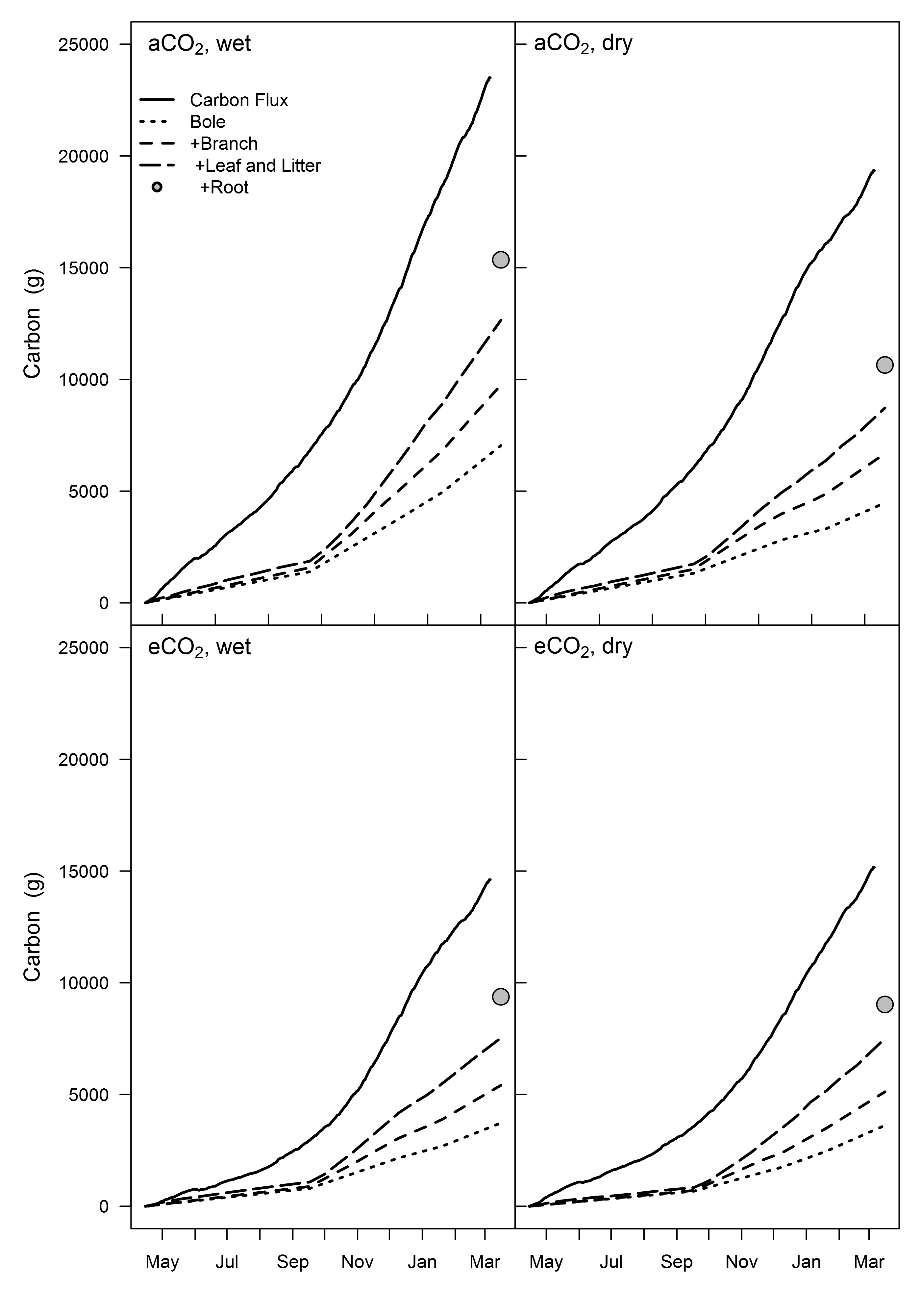
# Figures

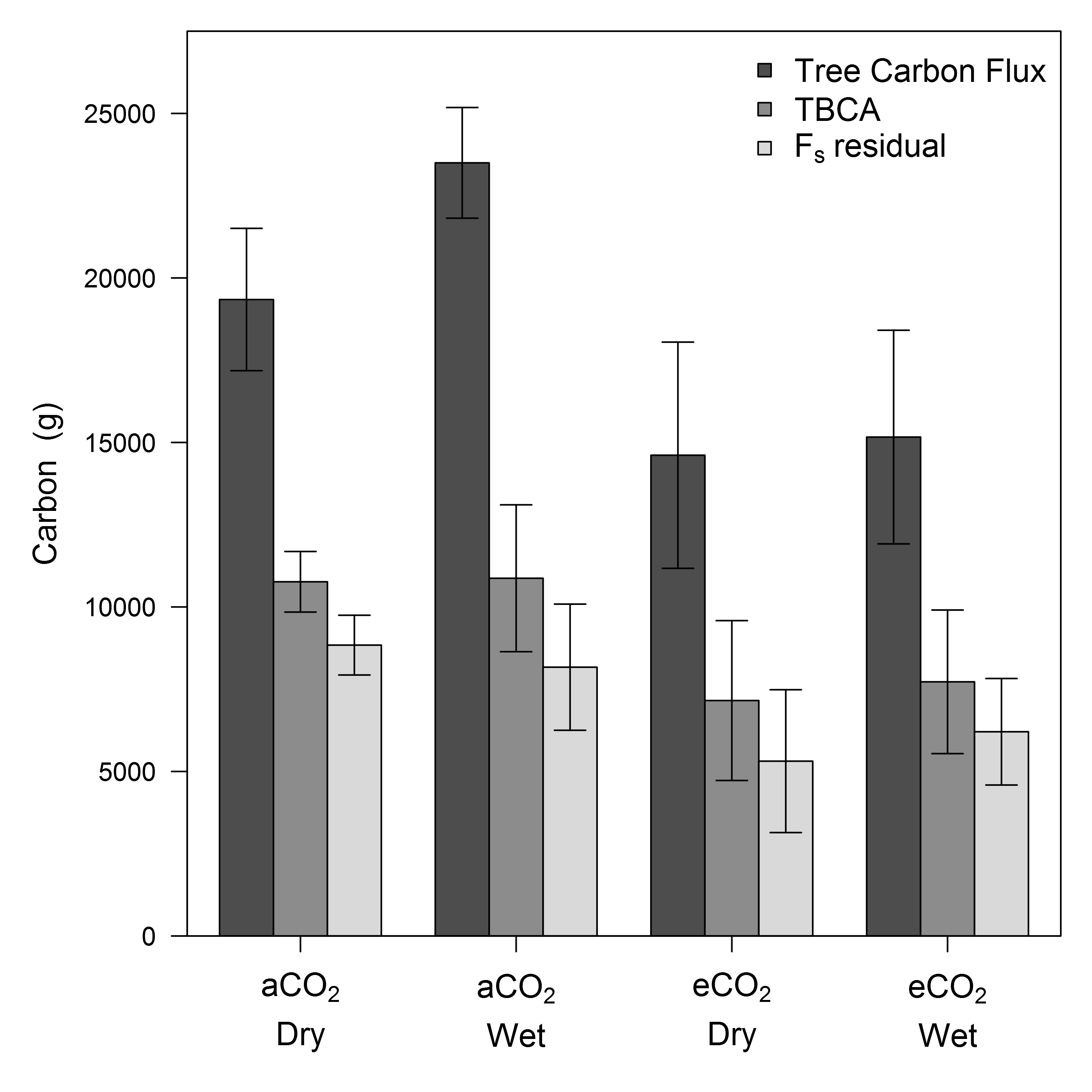
  
**Figure 1**.

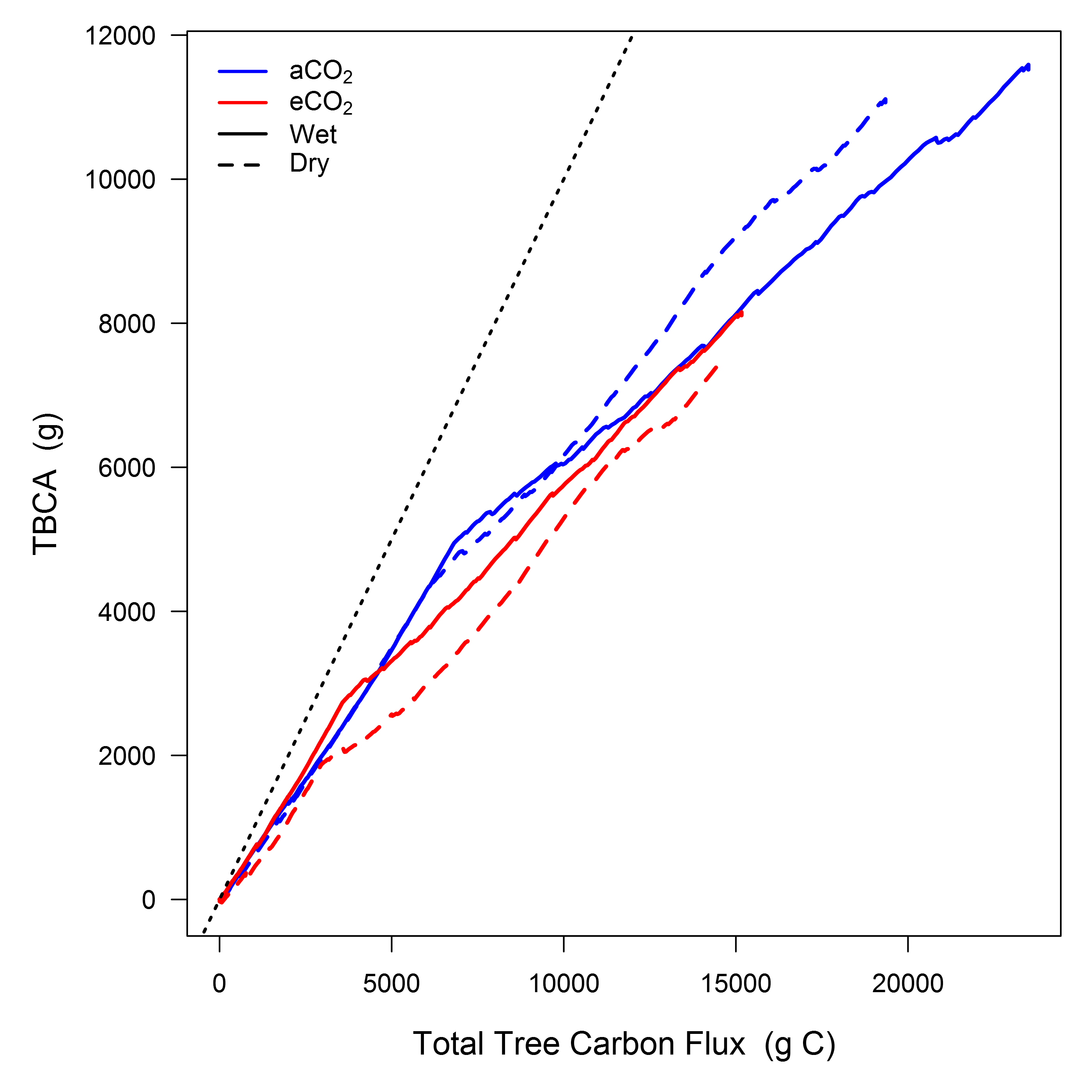
  
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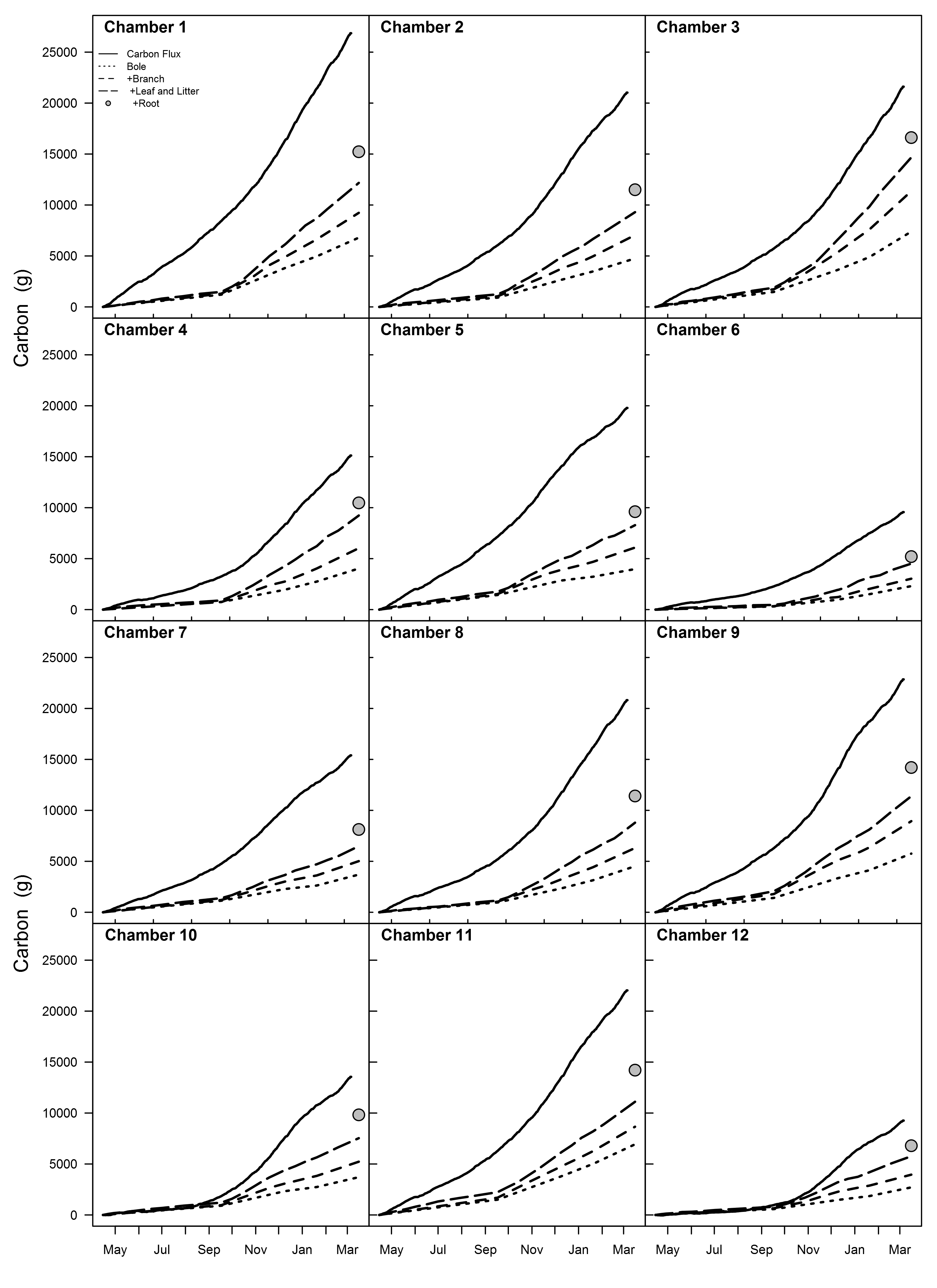
  
**Figure 4**.

  
**Figure 5**.

  
**Figure 6**.

  
**Figure 7**.

# Supporting Information

  
**Figure S1**.

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