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 empirical task and is thus challenging to capture in applied models of forest C cycling. Understanding how global change impacts the distribution of tree photosynthetic is an essential process in determining future terrestrial C balance. This study investigated how treatment manipulations of CO2 and drought affected the partitioning of photosynthetic C to biomass components of *Eucalyptus tereticornis* trees grown in climate-controlled whole tree chambers (WTC). It was hypothesized that that both drought and elevated CO2 would alter partitioning of C among biomass components. We then utilized the WTC design to provide measurements of aboveground net CO2 flux, which were expected to correlate to harvested tree C mass. For each WTC, total belowground C allocation was then calculated as the residual between the aboveground net CO2 flux and aboveground C mass. At the end of the experiment we observed that C allocation to aboveground woody tissue components was affected by the climate change treatments, while allocation to leaves and roots were not affected. The measured cumulative aboveground tree net CO2, after 18 months, correlated positively to both whole tree C mass and mean leaf area over the study period. Additionally, over 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. These results reveal how elevated CO2 and drought can impact the investment of photosynthetic C in a Eucalypt tree species and provide further empirical evidence to aid model predictions of forest productivity. The WTC also provide a novel framework to evaluate C allocation belowground.

# Key Words

carbon allocation, 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 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 Ca did not change. Alternatively, total belowground 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 C allocation is often estimated by subtracting the changes in C 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 C 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 C belowground.

Consequently, the representation of C allocation is rudimentary compared to photosynthesis (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 C to a particular component, are often used in process-based models of forest C 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 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 controlling temperature and air humidity at ambient conditions. 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 trees grown under elevated Ca were smaller than ambient trees and also 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 C allocation 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 to track the distribution of C above and belowground across the final eleven months of the experiment.

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

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

(3) Hypothesis about expectations from daily fluxes and 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 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 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.

## 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 over the final year of the experiment. 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, cumulative daily C fluxes (, g C d-1) were 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 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 (below) data. Leaf and litter C mass was calculated by multiplying harvested or estimated 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 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 reference diameter. 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 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 () 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

First, the basal area and length of every individual branch was from the final harvest was multipled to estimate individual branch volume, which was summed for each tree (Vbr, cm3). The product of two parameters, a geometric form factor from Makela et al. (1997) () and the total branch density (, g cm-3) was calculated as:

(1)

where Mbr is summed dry mass of harvested branches, corrects branch volume estimates to an intermediate shape between a cone and a cylinder and resprsents the combined density of wood and bark.

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 the product of and , specific to each WTC. We assumed that did not change 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:

(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.

## Total belowground carbon allocation

As the installation of chamber floors into each WTC separated the aboveground CO2 uptake from the soil CO2 efflux, total belowground C allocation (TBCA) at any time point was able to be calculated as:

(4)

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 at final harvest. 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 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 C mass balance were visualized by combining estimates of bole, branch, leaf and litterfall C with over the final 11 months of the experiment. The cumulative sum of , at any given time point, represented the net C uptake for each WTC. The allocation of C to boles and branches were seen by linear interpolation between survey measurements and the final harvest. Daily modeled estimates of leaf and litter C were then added to bole and branch C mass to estimate on any given day. Importantly, 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. 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 Ca and drought treatments at the final harvest were 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 C (R2 = 0.86, Figure 1,a) and (R2 = 0.78, Figure 1,b). was significantly reduced by 30.5 % under eCa (P = 0.043), while no effects of the drought treatment were detected. Similarly, both whole tree C and were reduced under eCa by ca. 32 % (both P < 0.03). Leaf area at the final harvest was significantly reduced by by 31.3% under eCa (p < 0.001), which was evident across the final eleven months 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 Ca and drought treatments (Table 1). There was a marginal interaction of eCa and drought on harvested bole C mass (p = 0.075). Elevated CO2 reduced bole C mass only in wet treatments (P = 0.041), while drought reduced bole C mass in ambient CO2 treatments only (P = 0.051). Total branch C mass was marginally reduced under eCa (P = 0.086) but was not affected by drought. 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.

Final LMF was increased by 15.2% under eCa (P = 0.031) but was 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 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 both TBCA and . Neither TBCA nor were affected by Ca or drought treatments (Figure 6). Total belowground C 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

**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 year 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), boles + branches (b) and roots (c) at final harvest as a function of tree size, via total tree carbon mass. Solid lines represent model fit for either LMF, SMF or RMF (R2 = -0.55, 0.55 and 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 cumulative aboveground 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.

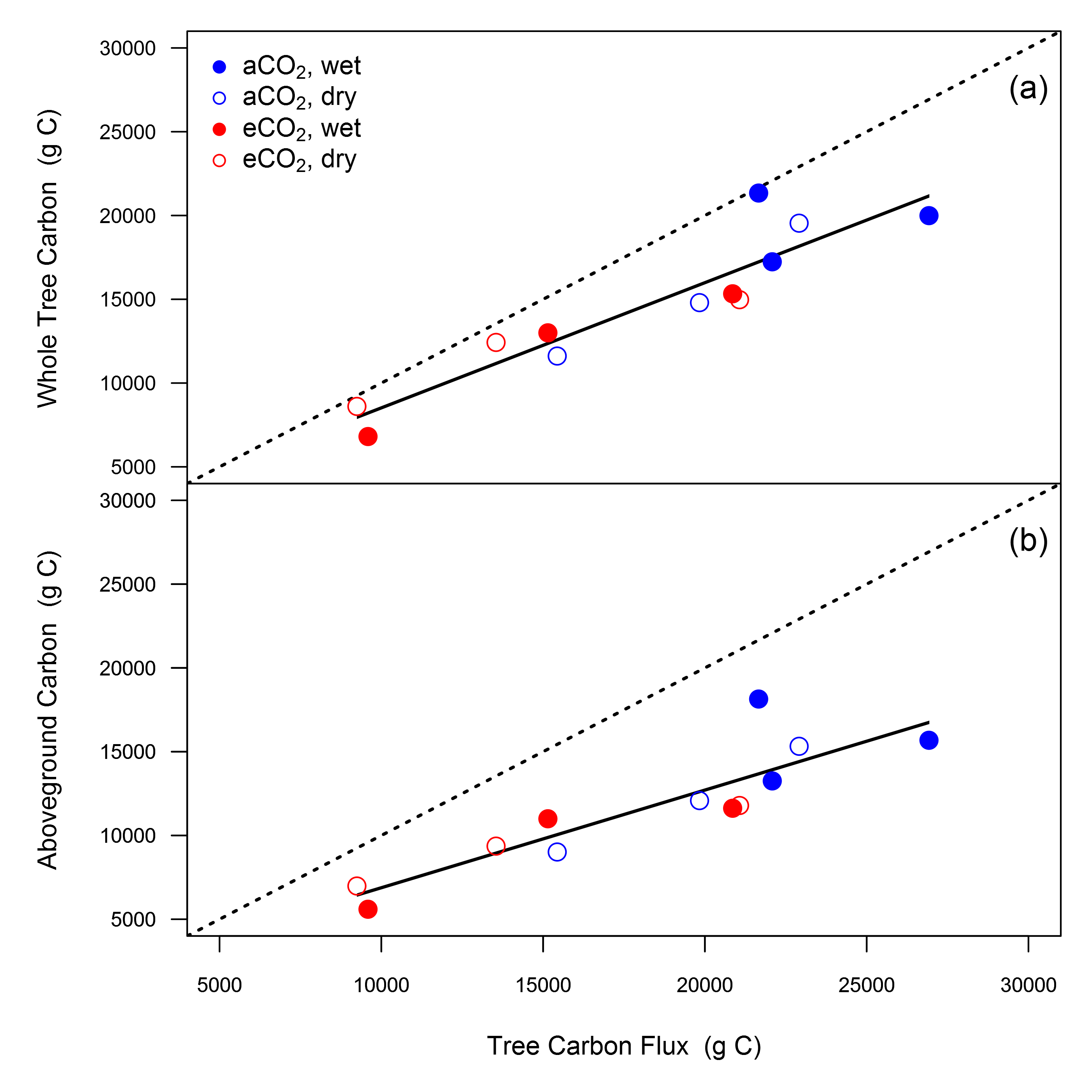
**Figure S1**. Cumulative aboveground C flux and additive C allocation of individual tree components from 2008-4-15 and 2009-3-16. Panels represent each individual WTC. Both C flux and tissue C allocation where set to 0 on 2008-4-15 in order to track the allocation of C in daily time steps. Total root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

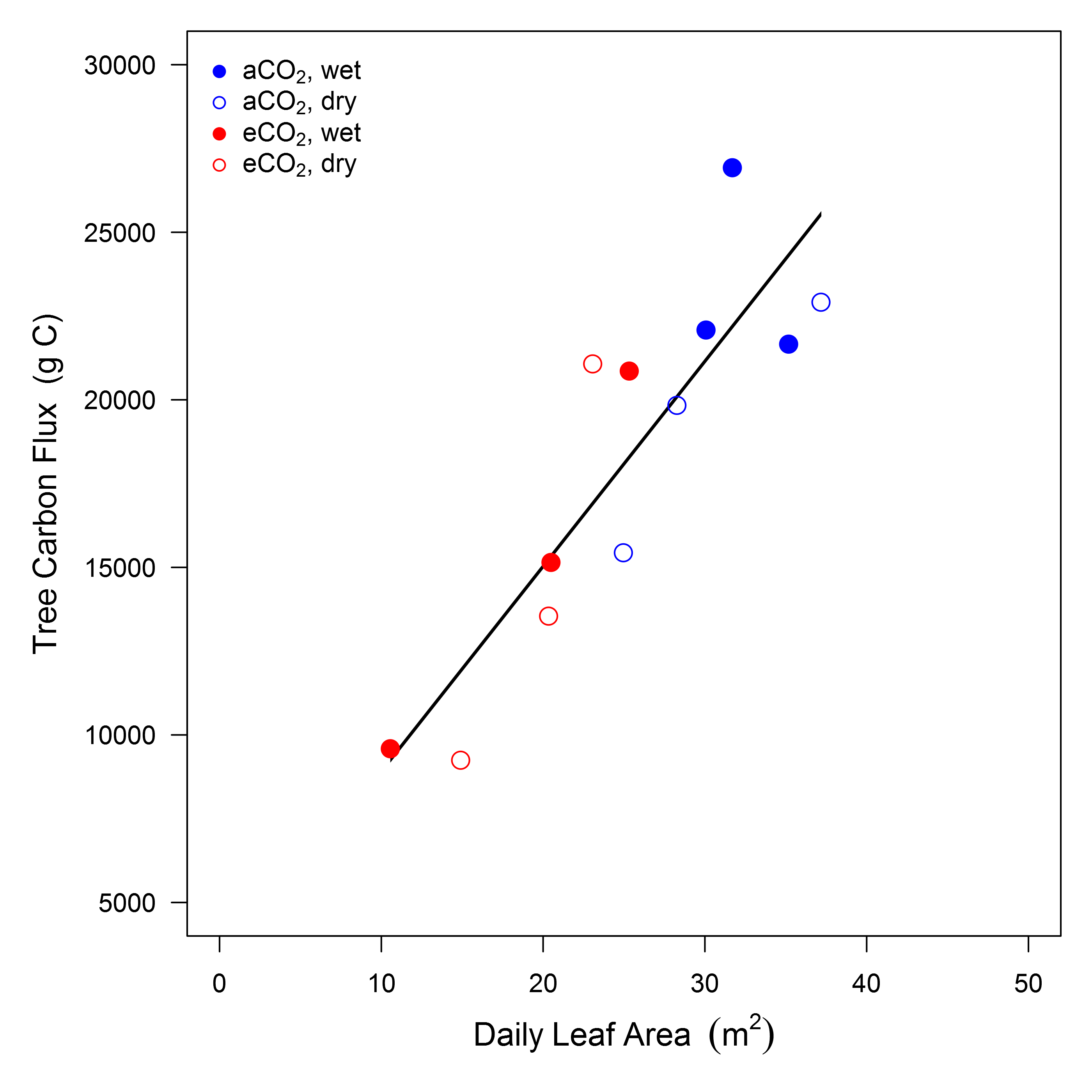
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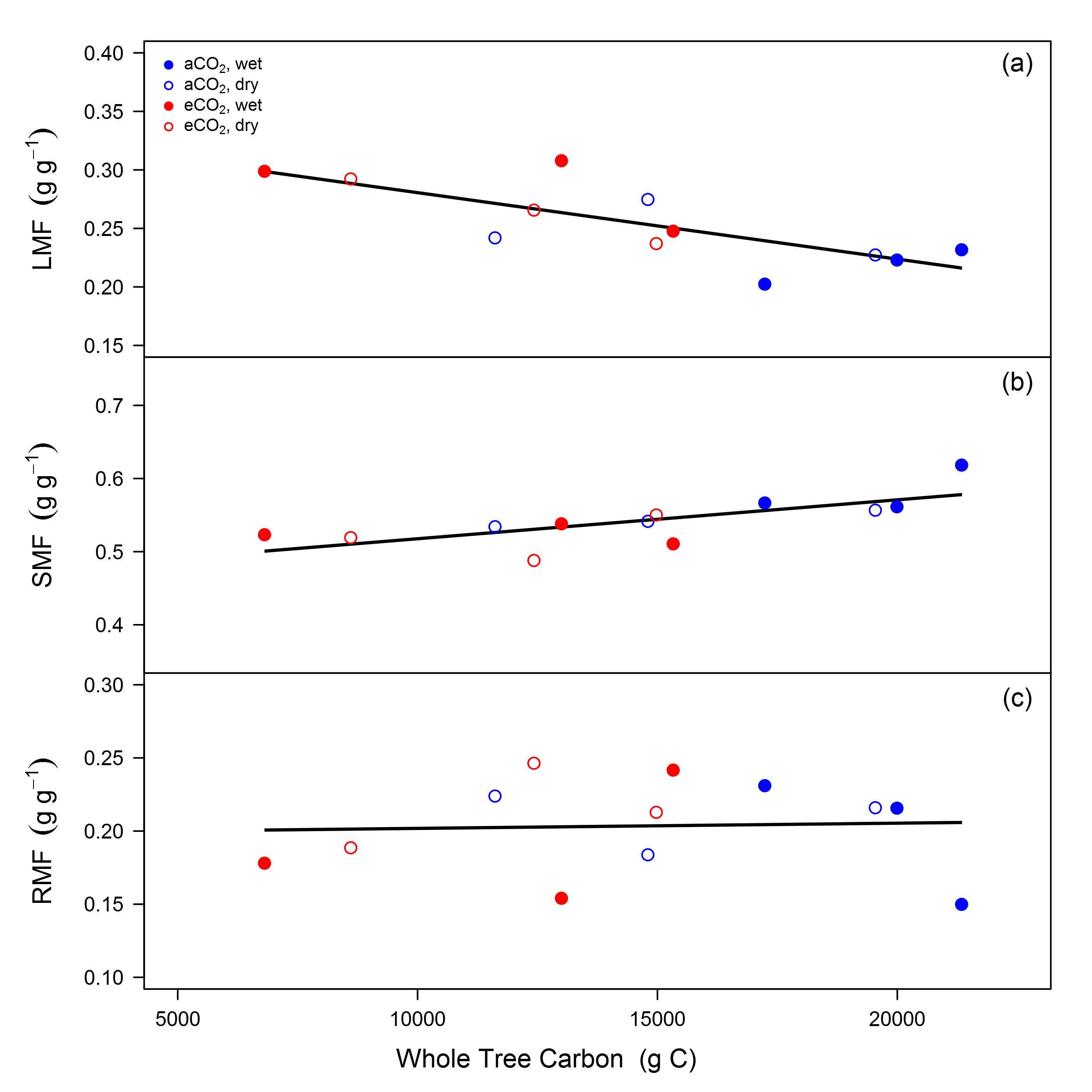
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| --- | --- | --- | --- | --- | --- | --- |
| **Treatment** | **Bole** | **Branch** | **Leaf** | **Litter** | **Root** | **Fc,t** |
| aCO2-dry | 5449.8 (715.6) b | 2915.9 (654.4) a | 2642.8 (370.7) a | 1129.8 (336.0) a | 3180.1 (521.0) a | 19394.2 (2169.5) a |
| aCO2-wet | 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 |
| CO2 effect (P) | 0.085 | 0.803 | 0.358 | 0.897 | 0.766 | 0.413 |
| Drought effect (P) | 0.085 | 0.803 | 0.358 | 0.897 | 0.766 | 0.413 |
| CO2 \* Drought (P) | 0.005 | 0.086 | 0.122 | 0.417 | 0.091 | 0.044 |

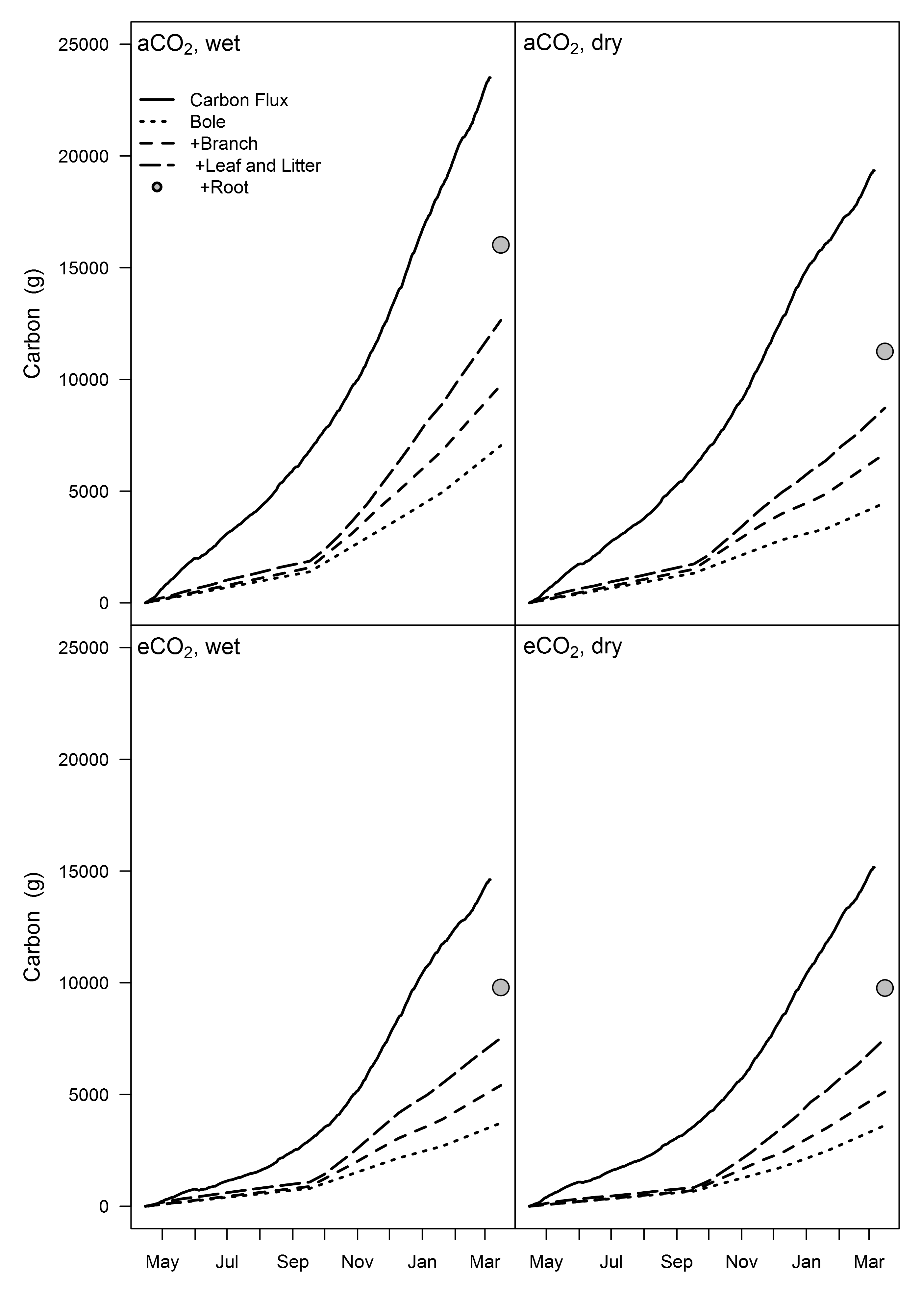
# Figures

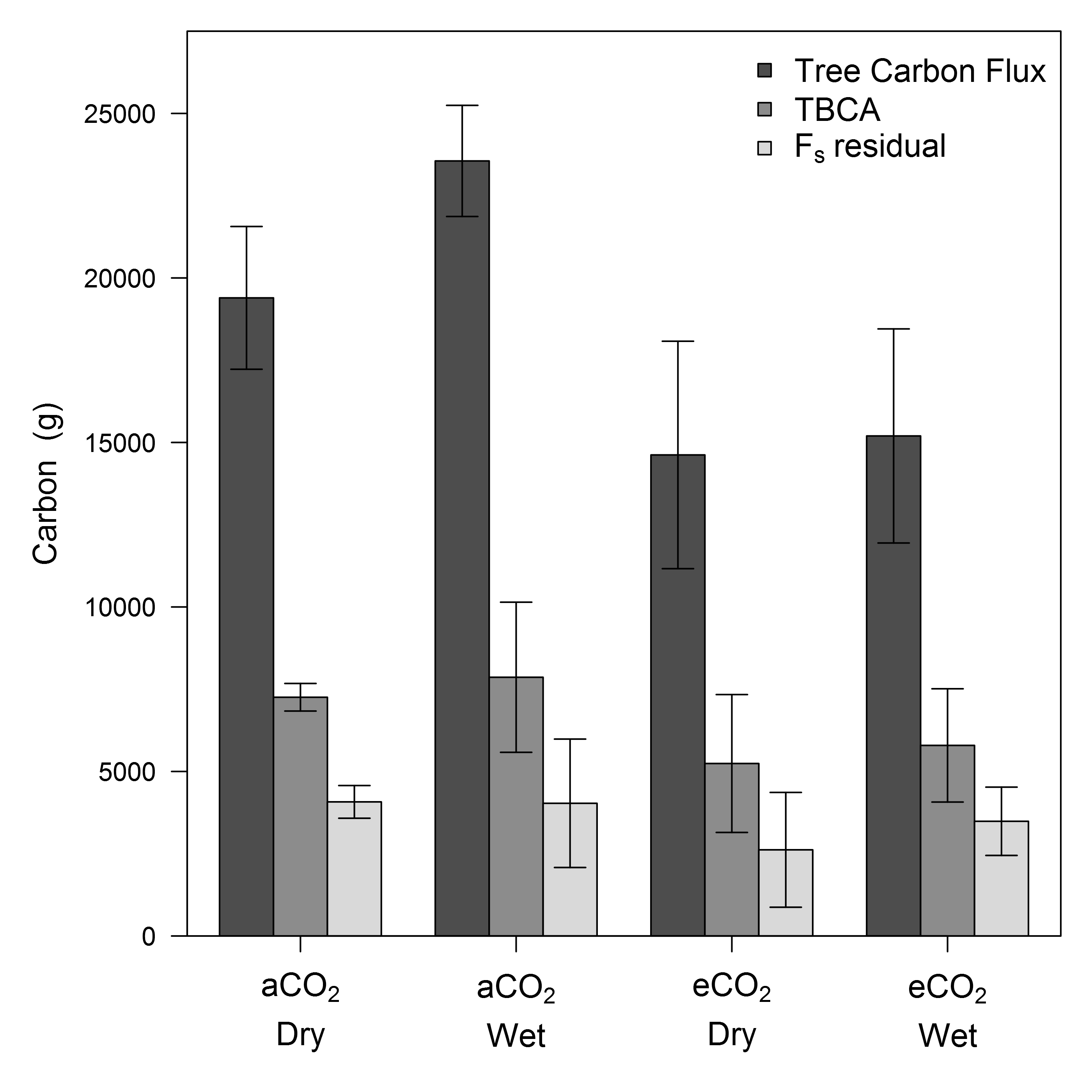
  
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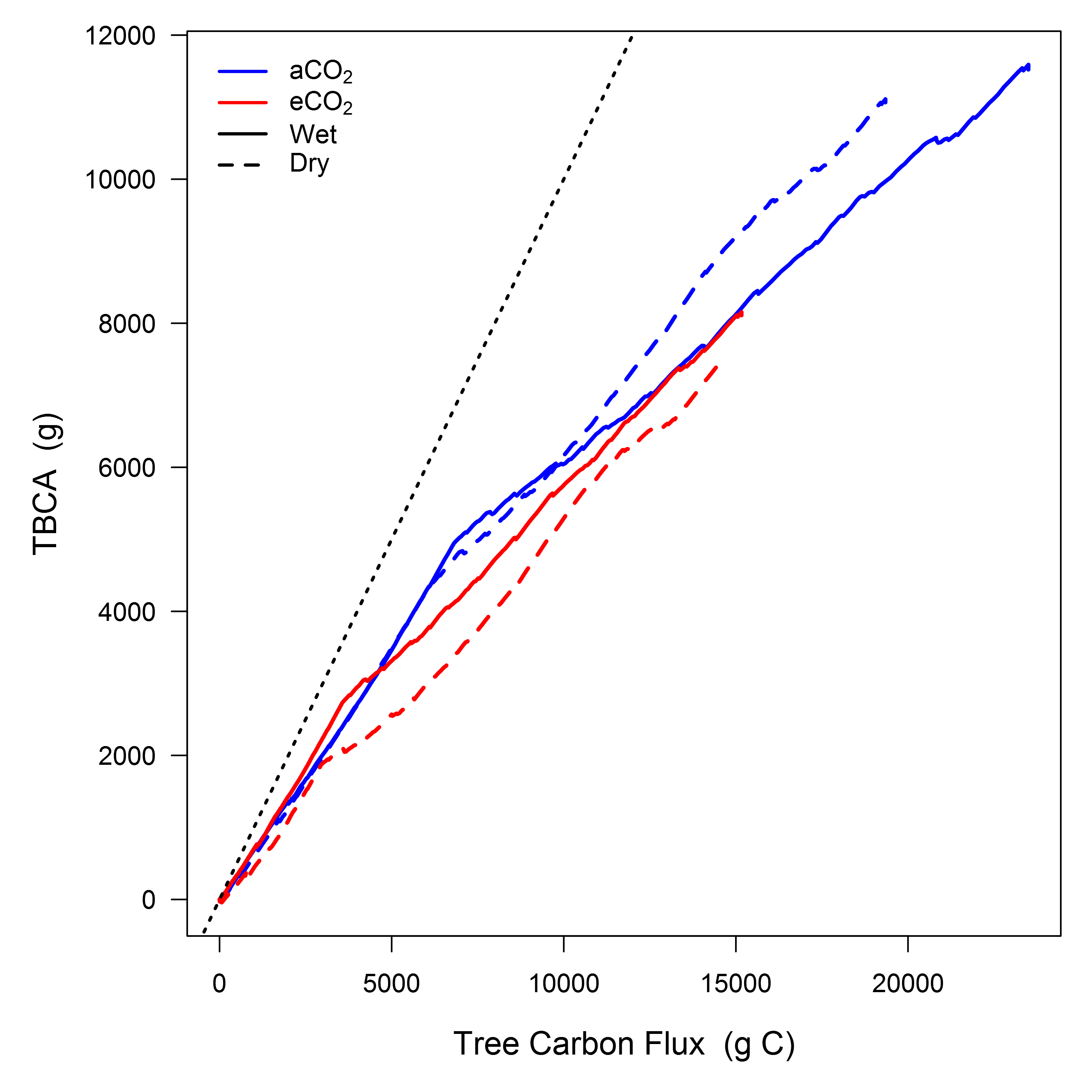
  
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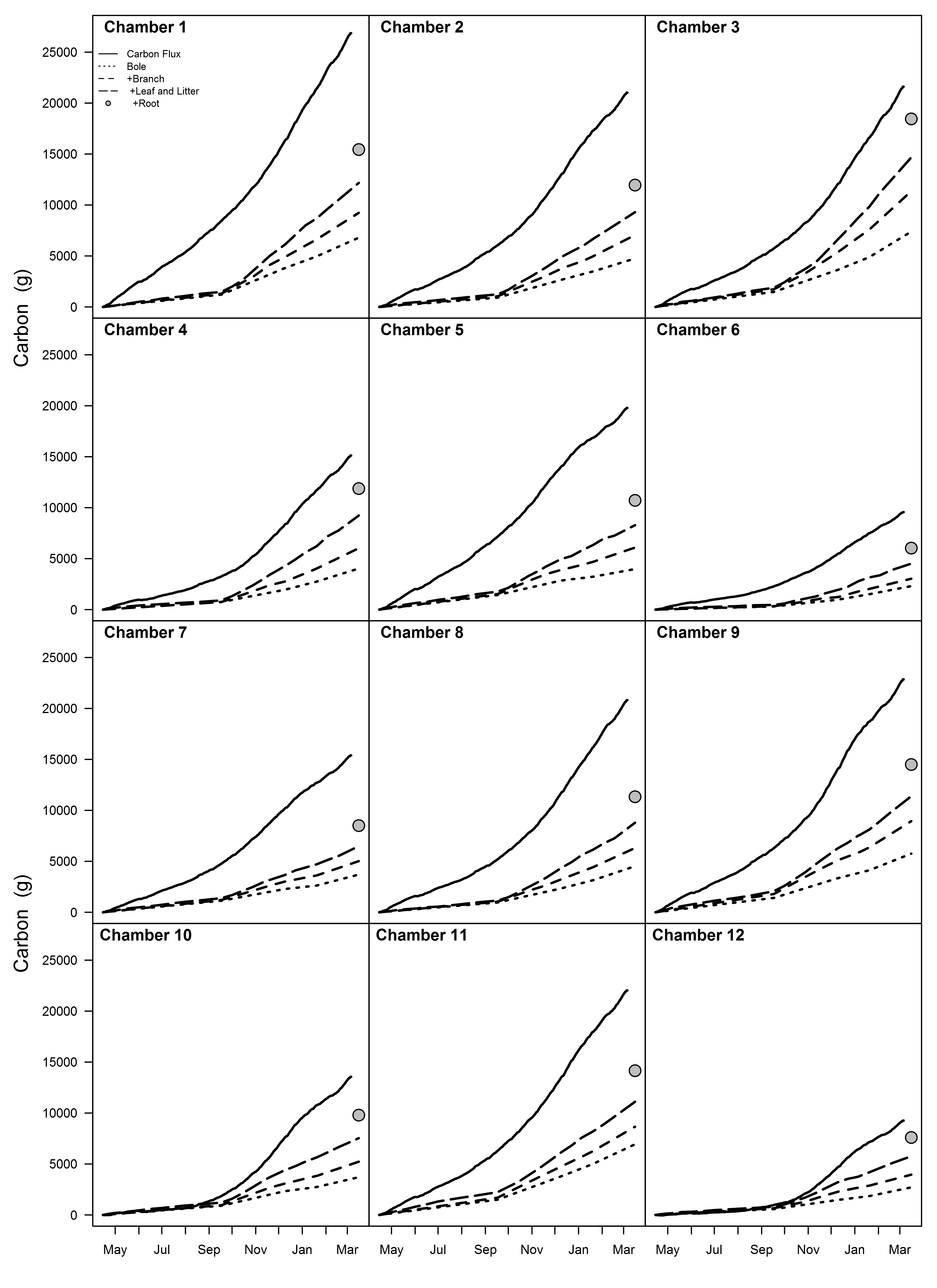
  
**Figure 4**.

  
**Figure 5**.

  
**Figure 6**.

  
**Figure 7**.

# Supporting Information

  
**Figure S1**.

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