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).

Variation in C allocation responses to environmental change combined with a lack of understanding of the mechanisms driving C allocation impede accurate modelling of the effects 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 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 predictions of C allocation are 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 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 compoents 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 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 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 droughted enviroments 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 require 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 probably not always the case. 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 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 track the distribution of C above and belowground across the final eleven months of the experiment.

(1) 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.

(2) 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.

(3) As shifts in partitioning to root biomass were hypothesized, we expected TBCA to vary through time as cumultaive tree C flux was 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

## 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 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 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 from March 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 C fluxes (, g C d-1) 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 (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 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 () 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 multiplied to estimate individual branch volume, which was summed for each tree (Vbr, cm3). The product of two parameters, a geometric form factor from Mäkelä 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, 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.

## 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 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. 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.

## Mass balance relationships between and C 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 final . At the end of the time 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). 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 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. Similarly, both whole tree C and from the final harvest were reduced under eCa by ca. 32 % (both P < 0.03). Integrated over the final 11 months of the experiment, 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), which was observed 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, at then end of the experiment, was affected differentially by the Ca and drought treatments (Table 1). There was a marginal interaction of eCa and drought on 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. When the aboveground woody compoents were combined (boles+branches) abovegrond wood C mass was reduced 37% under eCa (P = 0.0151). 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 by the Ca and drought treatments. 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 4b). Root mass fraction was not affected by either treatment and was not correlated to whole tree C (Figure 4c). Integrated over the final 11 months of the experiment, LMF was negatively correlated with adjusted (R2 = -0.54, P = 0.006). Niether SMF nor RMF were correlated with adjusted F[c,t] during this time period.

## 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

## TBCA

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).

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**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 = -0.57, 0.52 and 0.02, 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.

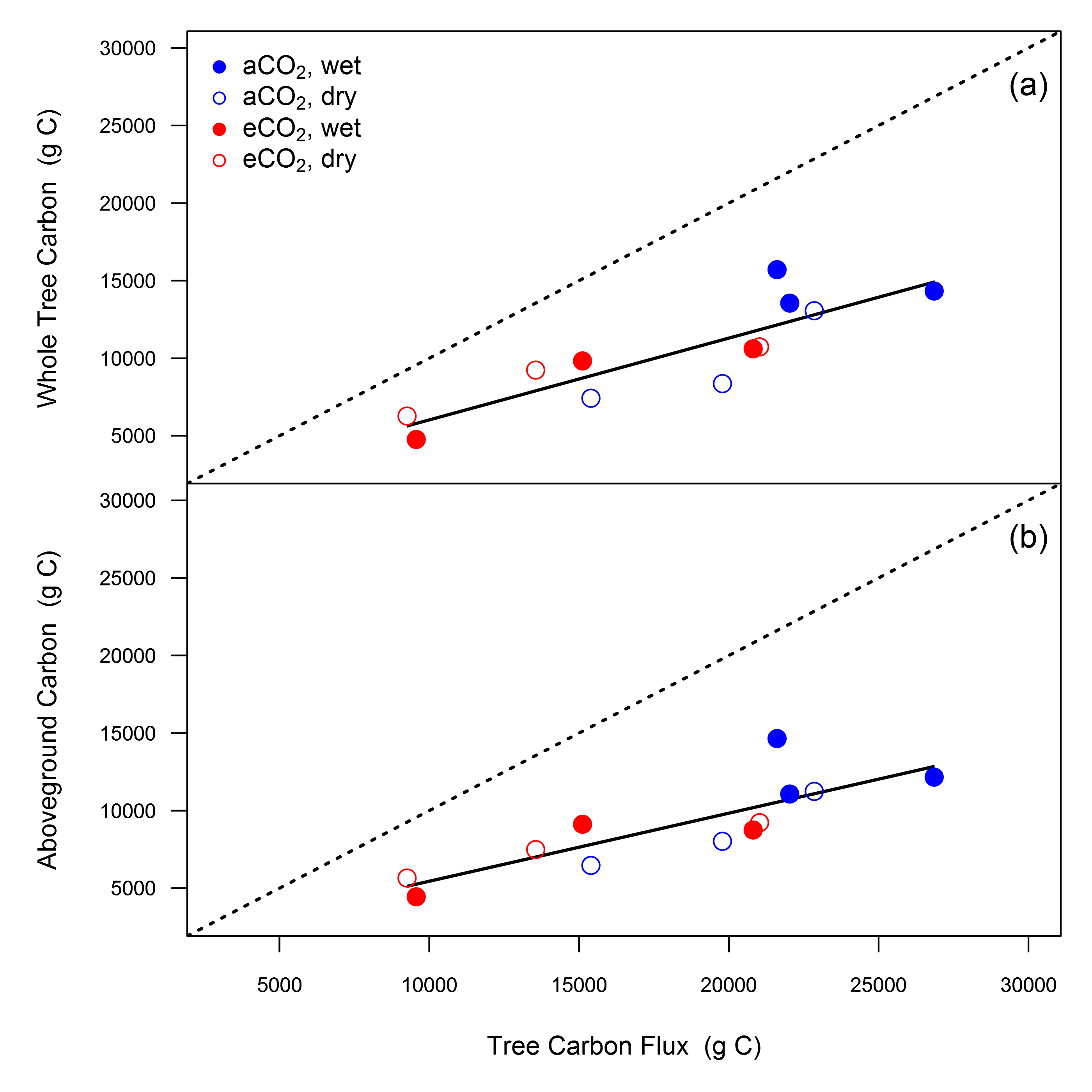
**Figure S1**. Cumulative aboveground C flux and additive C allocation of individual tree components from 2008-4-15 and 2009-3-16. Panels represent each individual WTC. Both C flux and tissue C allocation where set to 0 on 2008-4-15 in order to track the allocation of C in daily time steps. Total root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

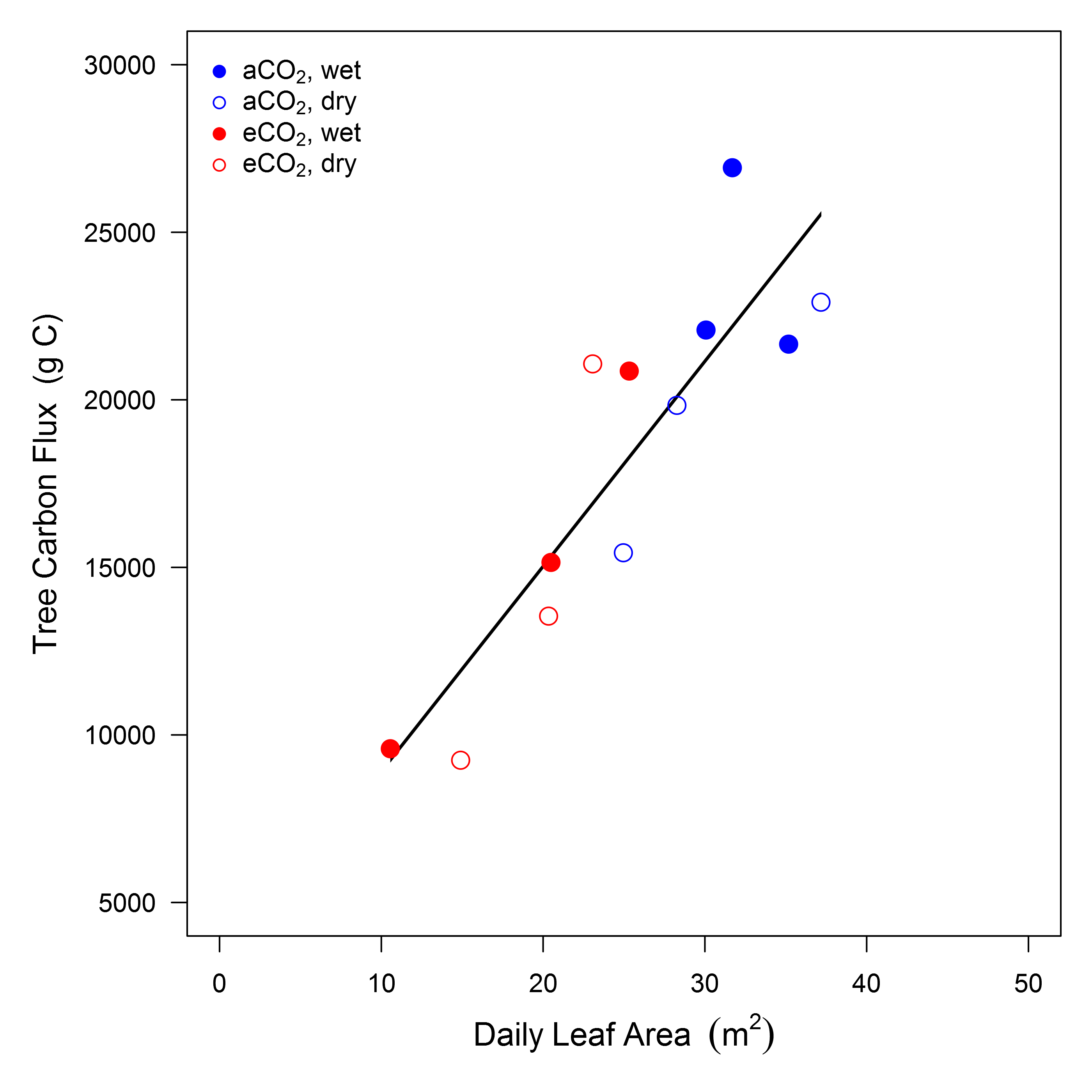
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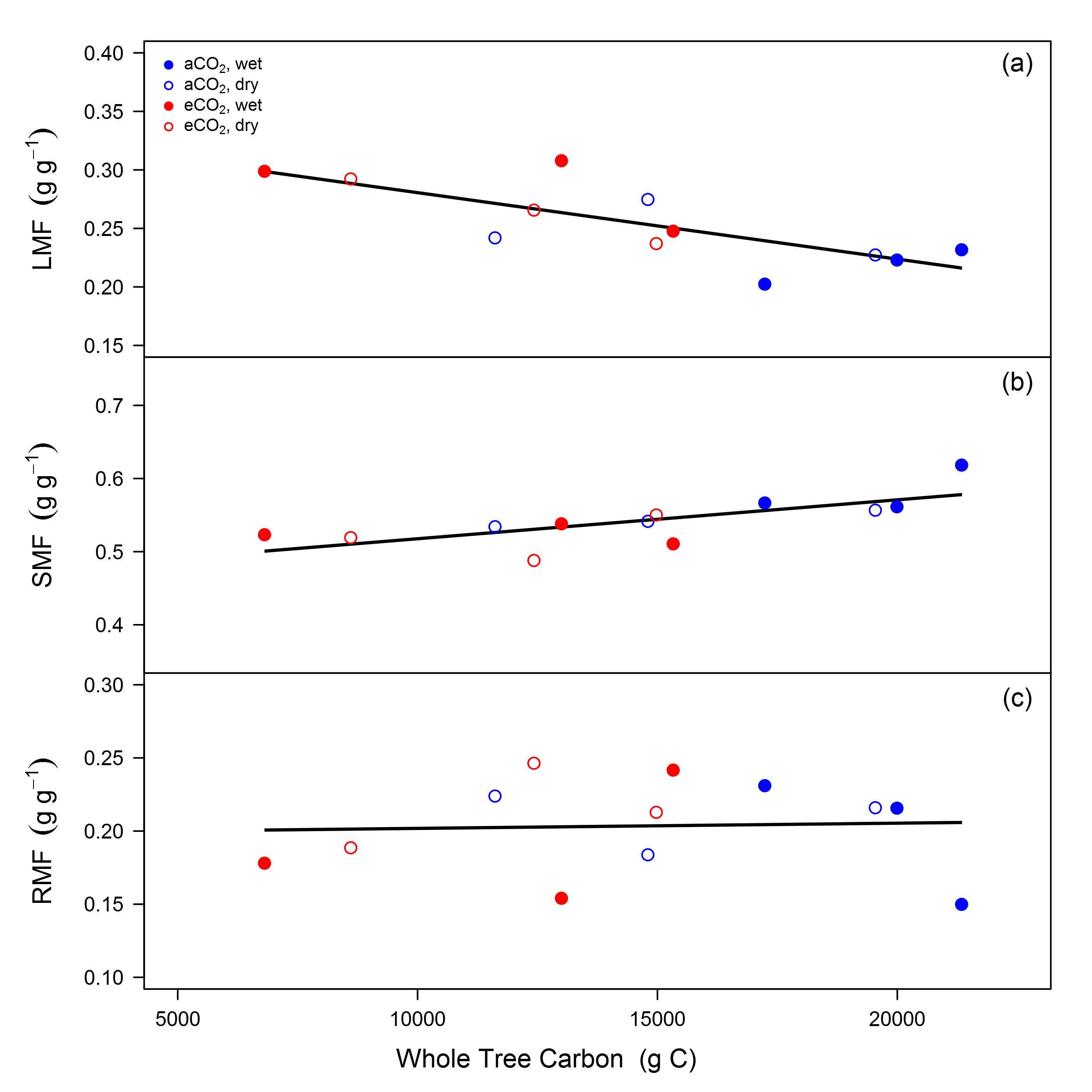
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| --- | --- | --- | --- | --- | --- | --- |
| **Treatment** | **Bole** | **Branch** | **Leaf** | **Litter** | **Root** | **Fc,t** |
| aCO2-dry | 5449.8 (715.6) b | 2915.9 (654.4) a | 2642.8 (370.7) a | 1129.8 (336.0) a | 3180.1 (521.0) a | 19394.2 (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 |

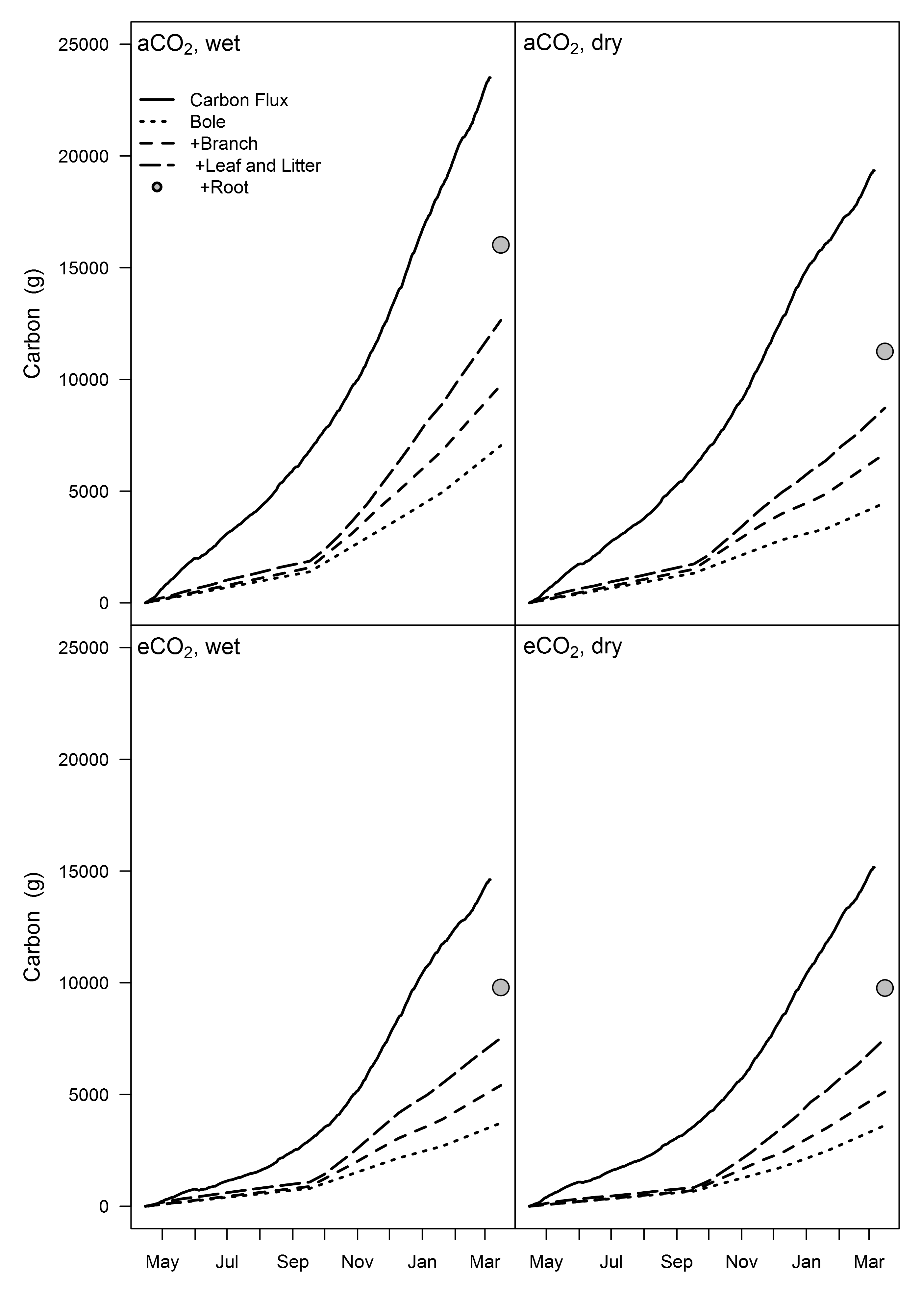
# Figures

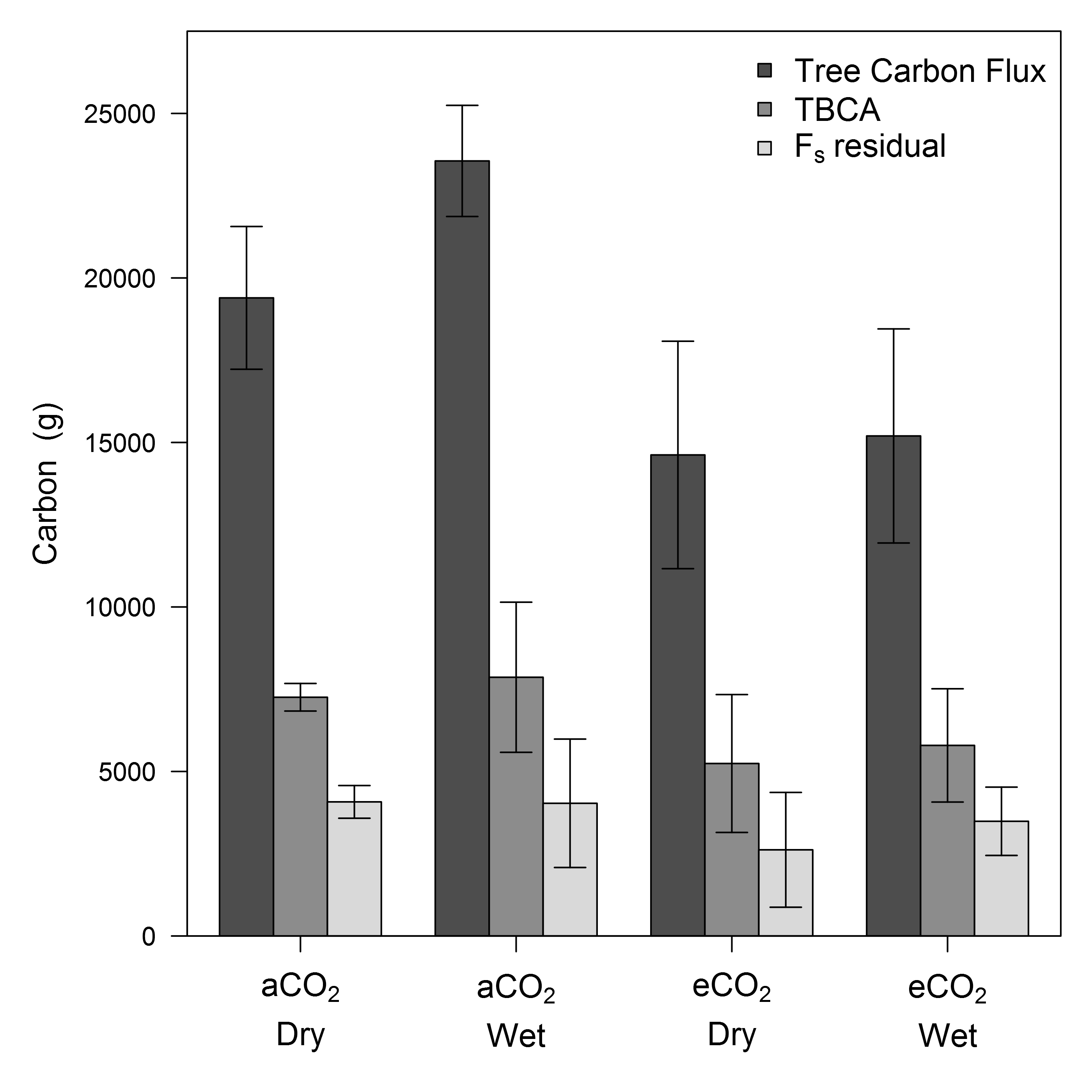
  
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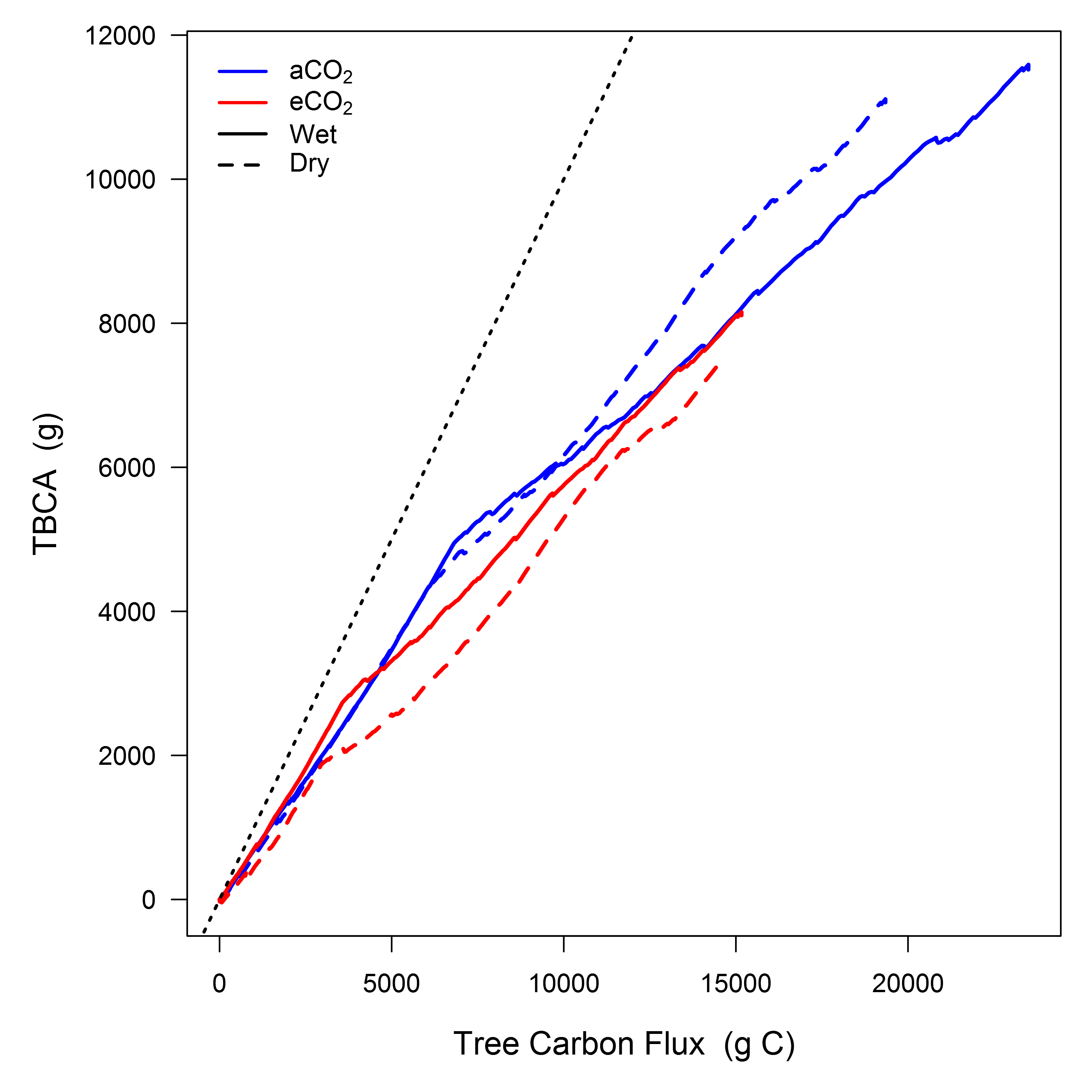
  
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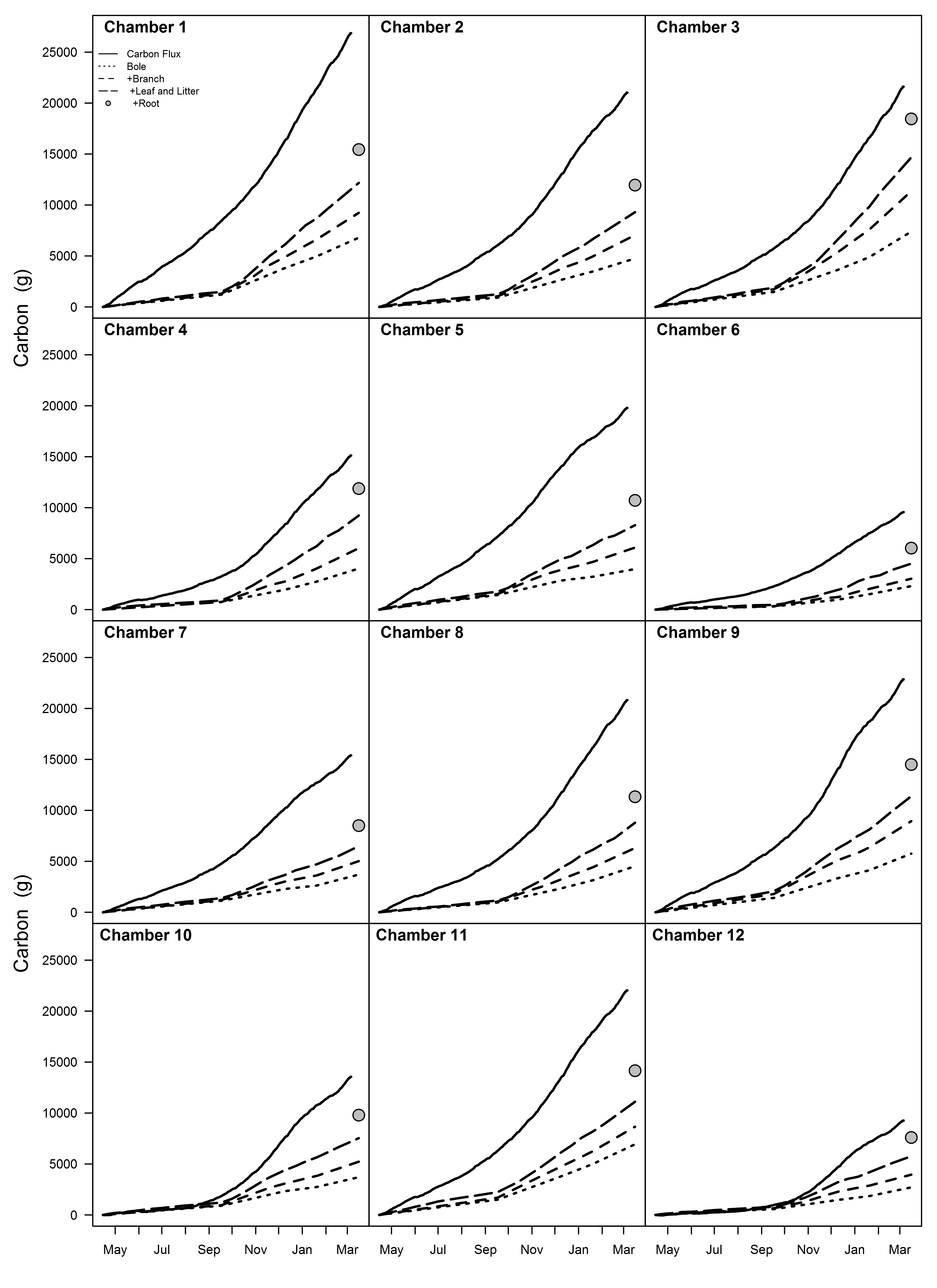
  
**Figure 4**.

  
**Figure 5**.

  
**Figure 6**.

  
**Figure 7**.

# Supporting Information

  
**Figure S1**.

# References

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

Anderegg WRL (2012) Complex aspen forest carbon and root dynamics during drought. Climatic Change 111:983–991.

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.

Bradford KJ, Hsiao TC (1982) Physiological responses to moderate water stress. In: Physiological plant ecology iI. Springer, pp 263–324.

Brando PM, Nepstad DC, Davidson EA, Trumbore SE, Ray D, Camargo P (2008) Drought effects on litterfall, wood production and belowground carbon cycling in an Amazon forest: results of a throughfall reduction experiment. Philosophical Transactions of the Royal Society B: Biological Sciences 363:1839–1848.

Broeckx LS, Verlinden MS, Berhongaray G, Zona D, Fichot R, Ceulemans R (2014) The effect of a dry spring on seasonal carbon allocation and vegetation dynamics in a poplar bioenergy plantation. GCB Bioenergy 6:473–487.

Cheng W, Fu S, Susfalk RB, Mitchell RJ (2005) Measuring tree root respiration using 13C natural abundance: rooting medium matters. New Phytologist 167:297–307.

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.

Fatichi S, Leuzinger S, Koerner C (2014) Moving beyond photosynthesis: from carbon source to sink-driven vegetation modeling. New Phytologist 201:1086–1095.

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.

Iversen CM (2010) Digging deeper: fine-root responses to rising atmospheric CO2 concentration in forested ecosystems. New Phytologist 186:346–357.

Iversen C, Norby R (2014) Terrestrial Plant Productivity and Carbon Allocation in a Changing Climate. In: Global environmental change. Springer, pp 297–316.

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.

Mäkelä A (2012) On guiding principles for carbon allocation in eco-physiological growth models. Tree physiology 32:644–647.

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.

Meier IC, Leuschner C (2008) Belowground drought response of European beech: fine root biomass and carbon partitioning in 14 mature stands across a precipitation gradient. Global Change Biology 14:2081–2095.

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.

Phillips RP, Erlitz Y, Bier R, Bernhardt ES (2008) New approach for capturing soluble root exudates in forest soils. Functional Ecology 22:990–999.

Phillips RP, Finzi AC, Bernhardt ES (2011) Enhanced root exudation induces microbial feedbacks to N cycling in a pine forest under long-term CO2 fumigation. Ecology letters 14:187–194.

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.

Schulze E-D, Robichaux RH, Grace J, Rundel PW, Ehleringer JR (1987) Plant water balance. BioScience:30–37.

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

Strand AE, Pritchard SG, McCormack ML, Davis MA, Oren R (2008) Irreconcilable differences: fine-root life spans and soil carbon persistence. Science 319:456–458.

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.