# Fertilization trajectory of the root crop *Raphanus sativus* across atmospheric $p$CO$_2$ estimates of the next 300 years

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## ABSTRACT

Plant biomass is known to increase in response to elevated atmospheric CO$_2$ concentration ($p$CO$_2$); how-ever, no experiments have quantified the trajectory of crop fertilization across the full range of $p$CO$_2$ levels estimated for the next 300 years. Here we quantify the above- and below-ground biomass response of *Raphanus sativus* (common radish) across eight $p$CO$_2$ levels ranging from 348 to 1791 ppmv. We observed a large net biomass increase of 58% above ground and 279% below ground. A large part of the net increase (38% of the above-ground and 53% of the below-ground) represented biomass fertilization at the high levels of $p$CO$_2$ (700–1791 ppmv) predicted if fossil fuel emissions continue unabated. The trajectory of below-ground fertilization in *R. sativus* greatly exceeded a trajectory based on extrapolation of previous experiments for plants grown at $p$CO$_2$ < 800 ppmv. Based on the experimental parameters used to grow these plants, we hypothesize that these experiments represent the maximum CO$_2$ fertilization that can be achieved for this plant growing under low light levels. If the below-ground biomass enhancement that we have quantified for *R. sativus* represents a generalized root-crop response that can be extrapolated to agricultural systems, below-ground fertilization under very high $p$CO$_2$ levels could dramatically augment crop production in some of the poorest nations of the world, provided that water resources are sufficient and sustainable.

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## 1. Introduction

The effects of climate change on agroecosystem sustainability and crop production are difficult to predict (Fuhrer, 2003), but have great implications for the global food supply (Schmidhuber and Tubiello, 2007). Tradeoffs between increased plant-tissue production (i.e., "CO$_2$ fertilization", Lobell and Field, 2008) and increased irrigation requirements resulting from climate change make the issue complex (Melillo et al., 1993; Tubiello et al., 2007). Current understanding of CO$_2$ fertilization is based on thousands of two-point experiments that have grown hundreds of plant species under ambient (300–420 ppmv) vs. slightly ele-vated (475–750 ppmv) $p$CO$_2$. Taken together, these experiments revealed an average total biomass increase of 20–54% (Kimball et al., 1993; Poorter, 1993; Wand et al., 1999; Poorter and Navas, 2003; Ainsworth and Long, 2005). The elevated $p$CO$_2$ levels used for these plant-growth experiments generally ranged from 475 to 750 ppmv, and were based on early projections for the year 2100 (Houghton et al., 1992); recent projections include $p$CO$_2$ esti-mates >750 ppmv (e.g., 560–820 ppmv for 2100, Nakicenovic and Swart, 2000). By the year 2300, $p$CO$_2$ levels may reach 1800 ppmv

if fossil fuel emissions continue unabated (Zachos et al., 2008). A simple extrapolation of $p$CO$_2$ data from Mauna Loa (1959–2008) NOAA/ESRL (2010), fitted to a second order polynomial equation ($R^2$ = 0.999), projects $p$CO$_2$ = 1847 ppmv for the year 2300. Although some two-point experiments have compared biomass in plants grown under ambient conditions to very high $p$CO$_2$ levels (i.e., 900–1200 ppmv) (Tognoni et al., 1966; Knecht, 1975; Luxmoore et al., 1986; Stuhlfauth et al., 1987; Riechers and Strain, 1988; Wheeler and Tibbitts, 1989; Vessey et al., 1990; Lord et al., 1993) and $p$CO$_2$ levels beyond those that plants have ever experienced on Earth (i.e., >10,000 ppm) (Park and Epstein, 1960; Schwarz and Strain, 1990; R.M. Wheeler et al., 1994), fertilization has not been quantified for any plant grown under the same conditions at mul-tiple levels of $p$CO$_2$ rise approaching the full range of greenhouse gas estimates for the next 300 years. The CO$_2$ emissions of the world's most populated countries are in an extreme state of flux (United Nations MDGI, 2010), which confers a large uncertainty to estimates for rising $p$CO$_2$ levels. For this reason, the true shape of the relationship between $p$CO$_2$ and plant biomass (i.e., the trajec-tory) must be known in order to accurately predict effects on crop production under multiple scenarios of $p$CO$_2$-rise.

The need for accurate root-crop fertilization trajectories is pressing: although production of root crops globally has increased more than 50% in the last 50 years (Godfray et al., 2010), the people most dependent on root-crop agriculture reside in the most impov-

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erished portions of the globe (Kates and Dasgupta, 2007; United Nations FAO, 2010). Ethiopia, one of the ten poorest and most malnourished nations of the world (United Nations Development Programme, 2009), relies on "roots and tubers" as the number-one commodity within its agriculture sector, which generates more than 50% of Ethiopia's gross domestic product (United Nations FAO). *Raphanus sativus* L. (Cherry Belle radish), in particular, is a crop of some importance. Each year, Americans spend sixty million dollars on grocery-store radishes, and the U.S. earns about 10 million dollars on its radish exports (Lucier and Jerardo, 2004). One-third of one's daily-recommended allowance of vitamin C can be gained from 20 calories of radish, at a cost of just eleven cents to the U.S. consumer (Otten et al., 2006). Radishes have the potential to be a highly sustainable crop: they grow to marketable size in three weeks, can be irrigated with wastewater (Bakhsh and Hassan, 2005), exist as several disease-resistant wild-types (Snow and Campbell, 2005), and *Raphanus* seed-oil has been proposed as a biofuel (Domingos et al., 2008).

Here we report the above- and below-ground biomass response and carbon stable isotope values for 132 *R. sativus* plants grown across eight carbon dioxide levels ranging from 348 to 1791 ppmv (Table S1) using established growth-chamber techniques (Jahren et al., 2008). We chose the herbaceous plant *R. sativus* based on its long-standing use as a model plant for environmental experiments (Kostka-Rick and Manning, 1993) and its classification in the Brassicaceae family with *Arabidopsis*, which has served as a model for examinations of the genetic basis of responses to elevated $pCO_2$ (Li et al., 2008). The response of *Raphanus* spp. to estimates of continued $pCO_2$ rise may serve as a harbinger for root crops as we contrast the 21st-century results of Global Change with its 20th-century predictions.

## 2. Materials and methods

### 2.1. Growth conditions

*R. sativus* (Harris Seeds of Rochester, ID # 0071) were grown within positive-pressure Plexiglass chambers under controlled $pCO_2$, light, and temperature after the design described within (Jahren et al., 2008). Carbon dioxide levels were increased by bleeding pure cylinder $CO_2$ into the intake pipe where it mixed with the ambient air before reaching the growth chamber. For each chamber the $CO_2$ flow rate was precisely controlled with an inline needle valve, thus enabling enrichment of air to the desired concentration of $CO_2$. Air was exhausted through an upper pipe and vented through a fume hood. Complete atmospheric turnover occurred approximately once every 10.4 min. The eight $pCO_2$ levels (348, 388, 413, 426, 760, 1090, 1425, and 1791 ppmv) were maintained within 10% of the desired $pCO_2$ level during four weeks of growth (Fig. 1A). We grew sixteen to eighteen plants at each $pCO_2$ level, which is double the median number of plants harvested in 350 previous elevated-CO2 experiments (Poorter and Navas, 2003). Experiments consisted of five days of germination on damp paper in the dark under ambient $pCO_2$, followed by four weeks of growth in standard potting soil (Miracle-Gro Moisture Control). This timing was designed to capture maximum growth after the cotyledons ceased to function but before reproduction was initiated, to assess biomass at a commensurate developmental stage of harvest within previous experiments (Poorter and Navas, 2003). Fluorescent grow lamps (33-W GE Brightstik) on adjustable shelving provided up to 230 $\mu$mol m$^{-2}$ s$^{-1}$ photosynthetic photon flux (400–700 nm), as measured at the leaf surface. Lights were controlled by a diurnal timer (11.75 h on; 12.25 h off per 24-h cycle). Because the lights generated heat inside the chambers, higher light levels could not have been achieved without increasing the growing temperature
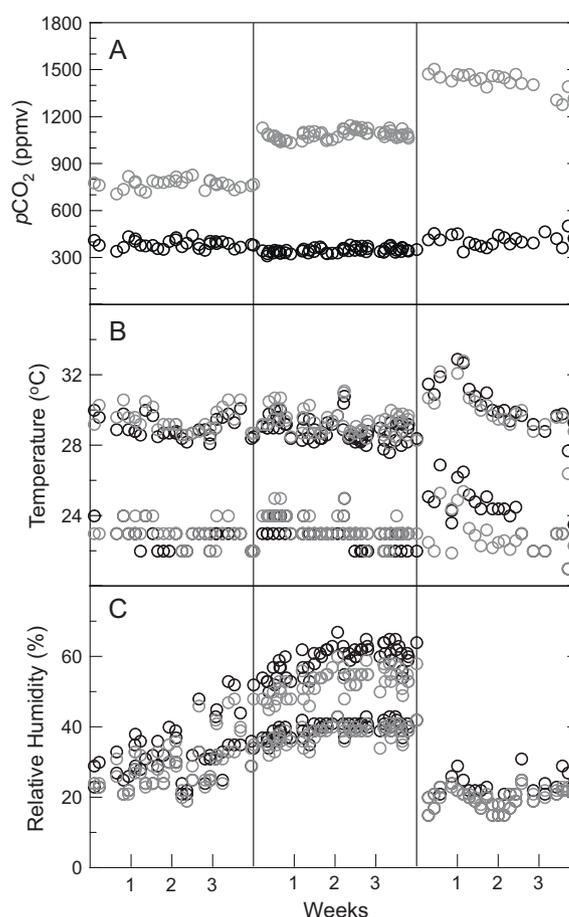


**Fig. 1.** $pCO_2$ (A), temperature (B), and relative humidity (C) conditions for three ambient (black) and three elevated (gray) $pCO_2$ experiments. Within the growth chambers, $pCO_2$ and temperature conditions were controlled; relative humidity fluctuated naturally. The mean and standard deviation for all experiments are presented in Table S1.

inside the chambers above the temperatures for maximum growth of *R. sativus* (Fig. 2 within Idso and Kimball, 1989). Mean daytime growing temperatures in the chambers averaged 23.3 °C or 29.5 °C (Fig. 1B) and matched temperatures shown for maximum growth of *R. sativus* (Fig. 2 within Idso and Kimball, 1989). Relative humidity was not controlled (average relative humidity was 29% and 37% for the high and low temperature regimes, respectively) (Fig. 1C); therefore, the affect of relative humidity on biomass was not determined. Wong (1993), however, found no significant difference in biomass between *R. sativus* plants grown at low (35%) and high (90%) relative humidity for ambient (350 ppmv) and slightly elevated (700 ppmv) $pCO_2$. Each plant occupied a separate soil container and was supplied with excess water, nitrogen, phosphorous, and trace nutrients. Soil was maintained at "field moist" conditions (Soil Survey Staff and Soil Conservation Service, 1999).

Plant growth within chambers has been documented to yield larger biomass relative to field growth (Baldy, 1986; Long et al., 2006); however, growth chamber design (Leadley and Drake, 1993; Edwards et al., 2009), computational methods (Poorter and Garnier, 1996), and experimental parameters such as light levels, temperature, relative humidity, water, nutrients, and pot size can effect plant growth results (Wong, 1979, 1993; Sionit et al., 1982; Sionit, 1983; Morison and Gifford, 1984; Zangerl and Bazzaz, 1984; Idso and Kimball, 1989; Bhattacharya et al., 1990; Farrar and Williams, 1991; Rogers et al., 1994; T.R. Wheeler et al., 1994; Schenk et al., 1996; Jablonski, 1997). Although our experiments were designed to maximize biomass at each $pCO_2$ level (optimal temperature, water,

**Table 1**
Growth parameters that can affect the $CO_2$ fertilization response.

| Parameter | This study | $CO_2$ fertilization response[a] |
|---|---|---|
| Chamber vs. field | Chamber | + |
| Light | 230 $\mu$mol m$^{-2}$ s$^{-1}$ PFF (400–700 nm) | − |
| Temperature | 23.3 and 29.5 °C (optimal[b]) | + |
| Relative humidity | 29 and 37% | x[c] |
| Water | Field moist[d] | + |
| Nutrients | Excess N, P, and trace elements | + |
| Pot size | 0.3 L | − |

[a] Maximum (+), limited (−), and no effect (x).
[b] Fig. 2 within Idso and Kimball (1989).
[c] Wong (1993).
[d] Soil Survey Staff and Soil Conservation Service (1999).

and nutrients for growth), it is possible that low light levels and pot artifacts lessened the $CO_2$ fertilization effect, especially at very high $pCO_2$ levels, by limiting the maximum, potential biomass (Table 1). Conversely, biomass enhancement of crops grown in agricultural fields is not limited by light levels or pot size, but may be limited by temperature, water, and nutrient stresses. Implications of resource limitations on $CO_2$ fertilization are discussed below.

### 2.2. Biomass assessment

After four weeks of chamber growth, above-ground tissues (stems and leaves) were harvested and separated from below-ground tissues (hypocotyl and roots), dried for 5 days at 60 °C, and weighed (uncertainty ±1 mg). We report all biomass weights in units of ln-transformed milligrams or as back-transformed values in units of milligrams (Table S3), as is the standard method for comparing plant mean dry weight (Poorter and Garnier, 1996).

We analyzed our biomass data in terms of a hyperbolic response, as routinely invoked for modeling $CO_2$ and light responses of photosynthesis in single leaves and whole plants (Lloyd and Farquhar, 1996; Nowak et al., 2004). In order to perform a direct and specific quantitative comparison to lower $pCO_2$ experiments, the data were plotted and fitted to a two-parameter rectangular hyperbola, after the method used by Hunt et al. (1991, 1993) for assessing the trajectory of the biomass response for 36 herbaceous species grown under $pCO_2$ levels ranging from 365 to 812 ppmv:

$$y = \frac{abx}{a + bx} \qquad (1)$$

where $y$ is the plant-yield variable (i.e., biomass); $x$ is the $pCO_2$ level; $a$ is the asymptote; and $b$ is the slope at $y = x = 100$ ppmv, the value used for $CO_2$ compensation point of dicotyledons (Ludlow and Jarvis, 1971; after Hunt et al., 1991). Hunt et al. (1991, 1993) defined the value $b$ as an overall index of $CO_2$ responsiveness: at low $b$ values the function approaches the asymptote slowly, at high $b$ more rapidly. Because the function is non-linear, fitted estimates of $a$ and $b$ were obtained by iterative optimization to maximize the correlation coefficient ($r$):

$$r = \sqrt{1 - \frac{\sum_{i=1}^{n}(y_i - yf_i)^2}{\sum_{i=1}^{n}(y_i - \bar{y})^2}} \qquad (2)$$

where $y_i$ is the average biomass value at each $pCO_2$ level, $yf_i$ is the fitted biomass value at each $pCO_2$ level, and $y_{avg}$ is the mean biomass value for all $pCO_2$ levels.

**Table 2**
Values for $a$, $b$, and $r$ (Eqs. (1) and (2), see text) calculated for Hunt et al. (1991, 1993) and this study.

| | $a$ | $b$ | $r$ |
|---|---|---|---|
| Hunt et al. (1991, 1993) | | | |
| Above[a] | 6.97 | 0.38 | −[b] |
| Below[c] | 6.40 | 0.38 | − |
| Total[a] | 7.41 | 0.46 | − |
| This study[d] | | | |
| Above | 5.89 | 0.23 | 0.88 |
| Below | 6.18 | 0.07 | 0.82 |
| Total | 6.68 | 0.16 | 0.86 |

[a] Calculated as the average $a$ and $b$ values reported in Hunt et al. (1991, 1993) for all responsive species (defined as having $b < 1$ for total biomass).
[b] Average biomass measurements for each species and $pCO_2$ level were not reported within Hunt et al. (1991, 1993); therefore, $r$-values could not be calculated.
[c] Hunt et al. (1991, 1993) did not report $a$ and $b$ values for below-ground biomass. We calculated the $a$ and $b$ values for below-ground biomass as the difference between the total- and above-ground biomass; total- and above-ground biomass were calculated for each $pCO_2$ level using Eq. (1) (see text). Fitted estimates of $a$ and $b$ were then obtained using Eq. (2), with $r = 1$.
[d] Using Eq. (2) (see text) fitted estimates of $a$ and $b$ were obtained by iterative optimization to maximize the correlation coefficient $r$.

### 2.3. Stable isotope analyses

After biomass assessment, above- and below-ground tissues were ground to a uniform powder in preparation for stable isotope analyses. The $\delta^{13}C$ values of plant tissues were analyzed using a Eurovector automated combustion system in conjunction with an Isoprime stable isotope mass spectrometer. All samples were introduced to the combustion system in pure tin capsules; stable isotope values are reported in standard $\delta$-notation (‰). The reporting standard is Vienna Pee Dee Formation limestone (VPDB) with $R = {}^{13}C/{}^{12}C = 0.011224$. Analytical uncertainty associated with each measurement was ±0.1‰. Presented values represent the average of three replicate capsules; the average isotopic variability of replicate capsules was ±0.15‰ for all tissues. Combustion also resulted in a quantification of percent carbon content in each sample.

We sampled gaseous $CO_2$ in each chamber using a pre-evacuated, 250-cm$^3$, glass vessel. We placed the vessel within the chamber we wished to sample, opened the stopcock, and let it equilibrate with the surrounding air for 10 min. We then concentrated and purified the $CO_2$ from the sampled atmosphere by slowly bleeding the air sample through a vacuum manifold, freezing any water into an ethanol/liquid-nitrogen cooled trap, and then freezing $CO_2$ into a series of liquid-nitrogen cooled traps, while simultaneously pumping away noncondensable gases. Pure $CO_2$ sample gas was analyzed for the $\delta^{13}CO_2$ value through the dual inlet of the mass spectrometer. We further purified one sample with 0.5 g of reduced copper at 450 °C for 2 h in order to remove $N_2O$ and thus test the effect of naturally occurring $N_2O$ on chamber $\delta^{13}CO_2$. We found no difference between the $\delta^{13}CO_2$ value of the sample reacted with reduced copper and the non-reacted sample.

## 3. Results

### 3.1. Increases in biomass

In keeping with the majority of the previous studies on $CO_2$ fertilization, we observed R. sativus grown to maturity under elevated $pCO_2$ levels to have greater total biomass than those grown under ambient atmospheric conditions (Fig. 2A). Using the hyperbolic model described in Section 2.2, we found that while the above-ground response ($b = 0.23$) was similar to the mean value of responsive (i.e., total biomass, $b < 1$) angiosperms ($b = 0.38$; $n = 23$)
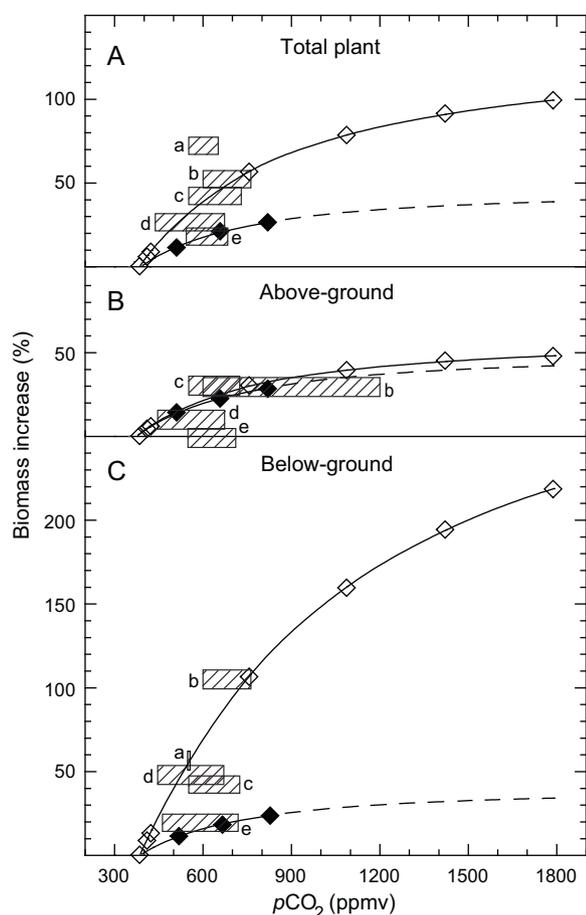
**Fig. 2.** Percent-biomass-increase observed for *R. sativus* across the full range of atmospheric $pCO_2$ levels estimated for the next 300 years (348–1791 ppmv) compared with previous results on root crops (a, *Daucus carota*, carrot; b, *Raphanus sativus*, radish; c, *Beta vulgaris*, sugar beet; d, *Ipomoea batatas*, sweet potato; e, *Solanum tuberosum*, potato) and herbaceous species (Hunt et al., 1991, 1993) at lower $pCO_2$ levels. Percent-biomass-increase curves for this study (open diamonds) were calculated from the fitted hyperbolic functions for biomass (Eqs. (1) and (2) within text) using an ambient $pCO_2$ level of 389 ppmv (present $pCO_2$ level). Percent-biomass-increase curves (closed diamonds) were calculated using Eq. (1) and the mean *a* and *b* values reported for 23 responsive (*b* < 1, total biomass) herbaceous species (Hunt et al., 1991, 1993). Open diamonds (this study) and closed diamonds (Hunt et al., 1991, 1993) mark $pCO_2$ levels under which the plants were grown; dashed lines extrapolate data from Hunt et al. (1991, 1993). Root crop data (shaded bars) were compiled from published data on dry biomass following the methods of Poorter (1993). Data were restricted as follows: (1) only data from the vegetative phase were used, (2) only experiments with control $pCO_2$-levels between 300 and 450 ppmv and elevated $pCO_2$-levels less than 2000 ppmv were used, in order to make a direct, quantitative comparison with data from this study, (3) for studies in which multiple environmental variables were tested (i.e., ozone, water availability, irradiance, etc.), biomass data were collected from experiments in which control plants grew best, and (4) for studies with multiple harvest dates, only data from the final harvest were used. These criteria resulted in a total of 127 observations of percent biomass increase (*n* = 38, above ground; *n* = 45, below ground; *n* = 44, total biomass) (see Table S2). Data for root crops extend the range of elevated $pCO_2$ levels tested and mark the average biomass increase, relative to ambient $pCO_2$ levels. (A) Total biomass (sugar beet, *n* = 14; carrot, *n* = 3; sweet potato, *n* = 5; radish, *n* = 10; potato, *n* = 12). Except for potato (e), total percent biomass increases greater for root crops (shaded bars) than non-crop species (closed diamonds). Note that the average, percent-total-biomass-increase at lower $pCO_2$ levels for *Raphanus* from previous studies (shaded bar, b) is similar to that observed in this study (open diamonds), but the percent increase in total biomass at very high $pCO_2$ levels observed in this study exceeds the extrapolated data of Hunt et al. (1991, 1993) (dashed curve). (B) The above-ground response for root crops (sugar beet, *n* = 10; sweet potato, *n* = 8; radish, *n* = 6; potato, *n* = 14) does not exceed the response of non-root species at any $pCO_2$ level. (C) Below-ground biomass fertilization for root crops (sugar beet, *n* = 10; carrot, *n* = 2; sweet potato, *n* = 5; radish, *n* = 6; potato, *n* = 22) at low $pCO_2$ levels (<800 ppmv) (except potato) greatly exceeds the average response of non-crops across the full range of $pCO_2$ levels; however, the difference between root and

(Hunt et al., 1991, 1993), the below-ground response was remarkable (*b* = 0.07) (Table 2).

Individual variability is inherent to all biological experiments; however the plant-to-plant biomass variability did not exceed what is commonly observed for plant experiments in general. Total-biomass variability for each set of growing conditions (measured as the standard deviation of the ln-transformed biomass data) averaged 0.29, which is nearly identical to the median variability in total biomass determined by Poorter and Navas (2003) for 700 herbaceous plants (0.28).

Percent biomass increase across the full spectrum of $pCO_2$ levels, calculated from the fitted biomass values, showed that the total biomass increase we observed for *R. sativus* at $pCO_2$ levels up to 760 ppmv was consistent with the average percent increase observed in ten experiments on *R. sativus* grown at ambient (330–386 ppmv) and elevated (600–761 ppmv) $pCO_2$ (Fig. 2A). Maximum biomass augmentation, however, occurred in below-ground tissues, which will likely have a major impact on the distribution of biomass within the plant. An increase in root-to-shoot ratio is a common observation in experiments that elevate $pCO_2$ to ~700 ppmv (Rogers et al., 1994; Rogers et al., 1996) resulting from increased root size (length, diameter, and dry weight) (Rogers et al., 1992), and has been observed in *R. sativus*, specifically (Overdieck et al., 1988; Barnes and Pfirrmann, 1992; Chu et al., 1992; Wong, 1993; Jablonski, 1997). The percent biomass increase was up to 58% and 279% for above- and below-ground tissues, respectively (Fig. 2B and C). Much of the net increase (38% for above- and 53% for below-ground biomass) occurred above 700 ppmv, i.e., above the average $pCO_2$ estimates for 2100 (Houghton et al., 1992) and most commonly used elevated $pCO_2$ level in two-point experiments (Poorter and Navas, 2003).

For above-ground tissues, the trajectory of percent biomass increase observed in our experiments up to ~1800 ppmv is identical to the trajectory of Hunt et al. (1991, 1993) for lower $pCO_2$ experiments (<800 ppm) (Fig. 2B). The trajectory that we observed for below-ground biomass increase was extremely high compared to other herbs (Fig. 2C), causing the trajectory for total biomass to similarly exceed extrapolation based on previous experiments (Fig. 2A). If we compare the fertilization trajectory we observed to the results of two-point studies on root crops, we see that the data for lower $pCO_2$ studies is within the range of our study for both above- and below-ground tissues (Fig. 2), and for very high $pCO_2$ levels, below-ground fertilization increases significantly.

### 3.2. Stable carbon isotope confirmation of growing conditions

Experiments were conducted under luxury conditions (i.e. excess water and nutrients) and temperature levels for optimal growth (Fig. 2 within Idso and Kimball, 1989; Wong, 1993) to allow us to measure maximum biomass enhancement. Nevertheless, it is important to show that lower biomass plants were not somehow less able to access water and nutrients. Multiple studies have shown that water, nitrogen, temperature, light, and other environmental stresses alter the net carbon isotopic fractionation ($\Delta$) between atmospheric $\delta^{13}CO_2$ and the resultant $\delta^{13}C$ value of plant-tissue (Ehleringer et al., 1986, 2002; Ehleringer and Cooper, 1988; Farquhar et al., 1989; Zimmerman and Ehleringer, 1990; Arens et al., 2000; Bowling et al., 2002; Yin et al., 2005; Aranda et al., 2007; Cernusak et al., 2009; Yin et al., 2009; Kranabetter et al., 2010). If environmental stress exerted an influence over biomass production

**Fig. 2.** non-root species is greatest at very high $pCO_2$ levels (>800 ppmv). In general, previous data for above-ground, below-ground, and total biomass for *Raphanus* grown under slightly elevated $pCO_2$ levels (shaded bars, b) are consistent with data from this study (open diamonds).
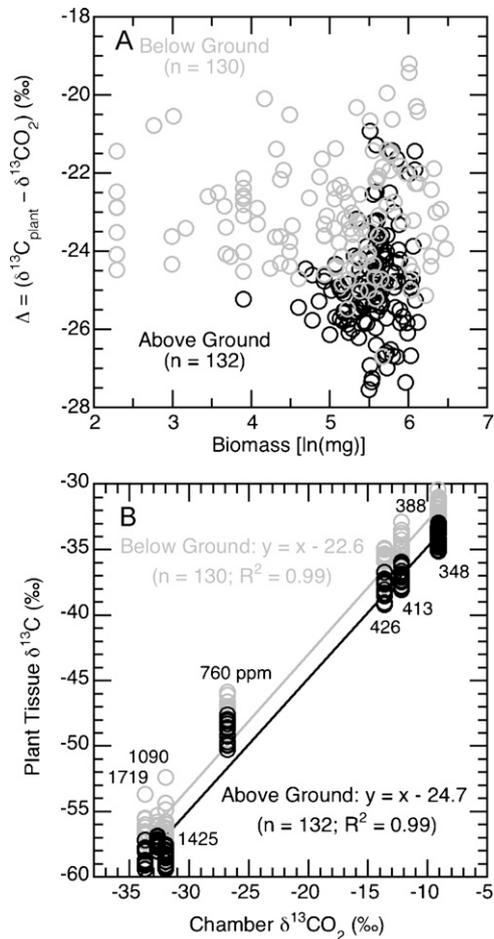
**Fig. 3.** Carbon isotope composition of plant tissue compared to plant biomass and to the carbon isotope composition of chamber $CO_2$. Lack of correlation between (A) the net carbon isotope fractionation ($\Delta = \delta^{13}C_{plant} - \delta^{13}CO_2$) and the amount of biomass produced contrasted with the strong correlation between (B) the carbon isotope composition of the plant tissue ($\delta^{13}C_{plant}$) and the carbon isotope composition of chamber $CO_2$ ($\delta^{13}CO_2$). Carbon isotope values are given in units of per mil (‰) relative to VPDB standard. Biomass is given as dry weight in units of ln-transformed milligrams [ln(mg)] after Hunt et al. (1991, 1993) and Poorter and Garnier (1996).

in our experiments, we would expect to see a relationship between the mass of tissue produced and the net carbon isotope fractionation between the plant and the atmosphere under which it grew. To the contrary, we saw no correlation (i.e., $R^2 < 0.1$; Fig. 3A). Elevated $CO_2$ may increase water-use efficiency (Eamus, 1991; Lawlor and Mitchell, 1991; Ceulemans and Mousseau, 1994; Jackson et al., 1994; Medlyn et al., 2001), but no isotopic evidence of water or nutrient stress or limitation was found in small or large plants; similarly, evidence for self-shading by leaves was not found. There was a strong correlation, however, between the carbon isotope composition of the plant tissue and the atmosphere under which it grew (i.e., $R^2 = 0.99$; Fig. 3B). This relationship was expected and is consistent with what we have shown for lower $pCO_2$ levels using similarly depleted cylinder-$CO_2$ to elevate the $CO_2$ levels within the chambers (Arens et al., 2000; Jahren et al., 2008).

## 4. Discussion

### 4.1. Implications for agriculture and sustainability

Other workers have shown that below-ground tissues for root crops may increase significantly more than non-root crops under slightly elevated $pCO_2$ levels (Idso et al., 1988) because the enlarged

hypocotyl provides a carbon sink (Overdieck et al., 1988; Miglietta et al., 2000); our work suggests that this effect will continue to augment at very high $pCO_2$ levels (>750 ppmv). Biomass enhancement due to elevated $pCO_2$ has been hypothesized to be ultimately subject to secondary limitation by nutrients (Ceulemans et al., 1999), in particular nitrogen (Finzi et al., 2007). However, increased allocation to below-ground tissues may enhance a plant's ability to acquire nitrogen, water, phosphorous and other micronutrients (Langley and Megonigal, 2010). Researchers have observed a decrease in protein concentration (Taub et al., 2008) and higher C:N ratios in plant tissues grown under elevated $pCO_2$ compared to tissues grown under ambient conditions due to increased nitrogen use efficiency at both low and high N supply (Overdieck et al., 1988; Conroy, 1992; Drake et al., 1997; Cotrufo et al., 1998; Taub and Wang, 2008). On average, however, N concentrations may decrease less in below-ground than above-ground tissues (Cotrufo et al., 1998). Other researchers have indicated that nutritive quality of crops is not expected to diminish due to rising $pCO_2$ levels (Idso and Idso, 2001). In our experiments, %C in tissues ($34.7 \pm 2.7$%C for above-ground tissue; $36.3 \pm 2.3$%C for below-ground tissue) was not correlated with $pCO_2$ growth-level, in agreement with previous studies (Overdieck and Reining, 1986; Overdieck et al., 1988); therefore, the biomass increase we observed did not carry a proportional increase in N-demand. Root growth also promotes mycorrhizal fungi that enhance availability and uptake of nutrients in the root zone (Lin et al., 2000; van Hees et al., 2006; Javaid, 2009), including in agricultural settings (Zhang et al., 2010). R. sativus (Brassicaceae) is part of the minority 8% of plant families that have no symbiotic association with mycorrhyzal fungi (Wang and Qiu, 2006); however, root exudates of Brassicaceae plants, including R. sativus specifically, have been shown to stimulate hyphal growth of mycorrhizal fungi (Zeng et al., 2003). Because fertilizer is a major and limiting agricultural expense within developing nations FAO (2008), increases in crop yield that do not require proportional fertilizer additions are a critical requirement for global sustainability.

The potential effect of increased below-ground biomass upon irrigation requirements is complex. It is reasonable to expect that any biomass enhancement will require an increase in plant-available water based on long-standing observations of the amount of water required for crop growth (e.g., 200–800 g of $H_2O$ used per production of 1 g of dry tissue, Lyon et al., 1952). However, water-use efficiency in plants increases under elevated $pCO_2$ due to a decrease in stomatal conductance (Eamus, 1991; Lawlor and Mitchell, 1991; Chu et al., 1992; Ceulemans and Mousseau, 1994; Jackson et al., 1994; Medlyn et al., 2001). In addition, plant roots increase mineral surface area below ground by breaking, fracturing, and aligning mineral grains (April and Keller, 1990), leading to increased residence time of soil water (Drever, 1994) and possibly buffering plants against droughts (Norby et al., 2004).

## 5. Conclusions

Our experiments showed that under slightly elevated $pCO_2$ (<760 ppmv), R. sativus biomass increased similarly to previous studies on crop and non-crop species. However, at higher $pCO_2$ levels, which include recent estimates for the year 2300 (Zachos et al., 2008), biomass enhancement in the primary, edible organ was much larger than what might be predicted from trajectories of non-crop species at lower-$pCO_2$ levels; the lower-$pCO_2$ portion of the trajectory we observed was consistent with two-point studies on root crops. If the dramatic biomass response to very high $pCO_2$ levels we have observed for R. sativus is shown to exist across other root crops (Miglietta et al., 2000) grown in the field, it may have implications for food production and future greenhouse gas emissions under the most current estimates of $pCO_2$

rise for the next 300 years. Yield increases of 135% in the last 50 years, due to agricultural intensification, have avoided emissions of 161 GtC, or 34% of the total carbon emitted by humans between 1850 and 2005 (Burney et al., 2010); further yield increase would continue this trend. Below-ground nutrient limitation could be inherently self-alleviating at elevated $pCO_2$ due to positive feedbacks between biomass production and water, nitrogen, and cation availability. The implications for global sustainability are complex: the top-twenty producing countries in the world sell $7.8 \times 10^9$ kg of roots and tubers each year (potatoes are excluded from this figure). Within these top-producers are four of the world's poorest nations, Ethiopia, Eritrea, the Democratic Republic of the Congo, and Timor-Leste (United Nations Development Programme, 2009), which produce 67% of the total above (=$5.2 \times 10^9$ kg), generating almost 600 million International Dollars of wealth per year (United Nations FAO, 2010). Needless to say, a doubling or tripling of below-ground crop tissue due to $CO_2$ fertilization would be welcome on both a nutritional and economic basis, especially given that the major grain crops of sub-Saharan Africa are C4 species (sorghum and maize), which show no $CO_2$ fertilization response in free-air concentration enrichment (FACE) experiments (Long et al., 2006). Even if some resource limitation is eased by processes inherent to below-ground fertilization, a concomitant increase in water requirement is unavoidable; however, >70% of total water use is already used for irrigated agriculture (Xiong et al., 2010). Locating additional water to support enhanced crop production is unlikely: Ethiopia and Eritrea have among the lowest amount of renewable freshwater resources per capita in Africa (United Nations Statistics Division, 2010). Even though estimates of future $pCO_2$ levels imply increased root-crop production, the regions most in need of these benefits may be unable to locate the expanded water resources necessary to truly profit.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.agee.2010.11.024.

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**Table S1**

Elevated $p\mathrm{CO_2}$ experiments performed.[a]

| $p\mathrm{CO_2}$ (ppmv)[b] | Temperature (°C)[b] | Humidity (%)[b] |
|---|---|---|
| 348 ± 17 | 23 ± 1 | 59 ± 6 |
| 348 ± 17 | 29 ± 2 | 40 ± 6 |
| 388 ± 26 | 23 ± 1 | 36 ± 8 |
| 388 ± 26 | 29 ± 1 | 27 ± 4 |
| 413 ± 39 | 23.9 ± 1.5 | 23 ± 3 |
| 413 ± 39 | 30.0 ± 1.8 | 20 ± 3 |
| 426 | 22.5 | –[c] |
| 426 | 29.7 | – |
| 760 ± 30 | 23 ± 1 | 32 ± 8 |
| 760 ± 30 | 29 ± 1 | 27 ± 5 |
| 1090 ± 30 | 23 ± 1 | 53 ± 5 |
| 1090 ± 30 | 29 ± 2 | 38 ± 7 |
| 1425 ± 59 | 22.8 ± 1.1 | 21 ± 2 |
| 1425 ± 59 | 29.7 ± 1.8 | 19 ± 3 |
| 1791 | 25.5 | – |
| 1791 | 30.1 | – |

[a]Eight plants were grown for each set of conditions, with the exception of $p\mathrm{CO_2}$ = 413 and 1425 ppmv for which 9 plants were growth in each experiment.
[b]All values are reported as the mean ± 1σ, as measured throughout the four-week experiment.
[c]Not measured.

**Table S2**
Percent biomass increase data.

| Species | Common name | Biomass part[a] | Control $p\mathrm{CO_2}$ (ppmv) | Elevated $p\mathrm{CO_2}$ (ppmv) | % biomass increase | Reference[c] |
|---|---|---|---|---|---|---|
| *Beta vulgaris* | sugar beet | AG | 332 | 725 | 49 | (Ziska et al., 1995) |
| *Beta vulgaris* | sugar beet | AG | 332 | 725 | 153 | (Ziska et al., 1995) |
| *Beta vulgaris* | sugar beet | AG | 332 | 725 | 28 | (Ziska et al., 1995) |
| *Beta vulgaris* | sugar beet | AG | 375 | 550 | -11 | (Manderscheid et al., 2010) |
| *Beta vulgaris* | sugar beet | AG | 375 | 550 | 5 | (Manderscheid et al., 2010) |
| *Beta vulgaris* | sugar beet | AG | 375 | 550 | 32 | (Manderscheid et al., 2010) |
| *Beta vulgaris* | sugar beet | AG | 375 | 550 | 20 | (Manderscheid et al., 2010) |
| *Beta vulgaris* | sugar beet | AG | 375 | 550 | 5 | (Manderscheid et al., 2010) |
| *Beta vulgaris* | sugar beet | AG | 375 | 550 | 4 | (Manderscheid et al., 2010) |
| *Beta vulgaris* | sugar beet | AG | 375 | 550 | 21 | (Manderscheid et al., 2010) |
| *Ipomoea batatas* | sweet potato | AG | 364 | 438 | 6 | (Bhattacharya et al., 1990) |
| *Ipomoea batatas* | sweet potato | AG | 364 | 666 | 9 | (Bhattacharya et al., 1990) |
| *Ipomoea batatas* | sweet potato | AG | 354 | 431 | 22 | (Biswas et al., 1996) |
| *Ipomoea batatas* | sweet potato | AG | 354 | 506 | 23 | (Biswas et al., 1996) |
| *Ipomoea batatas* | sweet potato | AG | 354 | 659 | 12 | (Biswas et al., 1996) |
| *Ipomoea batatas* | sweet potato | AG | 354 | 438 | -15 | (Biswas et al., 1996) |
| *Ipomoea batatas* | sweet potato | AG | 354 | 514 | -2 | (Biswas et al., 1996) |
| *Ipomoea batatas* | sweet potato | AG | 354 | 665 | 19 | (Biswas et al., 1996) |
| *Raphanus sativus* | radish | AG | 386 | 761 | 7 | (Barnes and Pfirrmann, 1992) |
| *Raphanus sativus* | radish | AG | 330 | 600 | 25 | (Chu et al., 1992) |
| *Raphanus sativus* | radish | AG | 350 | 700 | 8 | (Wong, 1993) |
| *Raphanus sativus* | radish | AG | 350 | 700 | 52 | (Wong, 1993) |
| *Raphanus sativus* | radish | AG | 350 | 650 | 22 | (Overdieck et al., 1988) |
| *Raphanus sativus* | radish | AG | 400 | 1200 | 66 | (Knecht, 1975) |
| *Solanum tuberosum* | potato | AG | 380 | 550 | -8 | (Högy and Fangmeier, 2009) |
| *Solanum tuberosum* | potato | AG | ambient[b] | 680 | -43 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | AG | ambient | 680 | -26 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | AG | ambient | 680 | -10 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | AG | ambient | 680 | -12 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | AG | ambient | 680 | -15 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | AG | ambient | 680 | 26 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | AG | ambient | 680 | -4 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | AG | ambient | 680 | -2 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | AG | ambient | 680 | 28 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | AG | 398 | 543 | 23 | (Donnelly et al., 2001) |
| *Solanum tuberosum* | potato | AG | 398 | 694 | 28 | (Donnelly et al., 2001) |
| *Solanum tuberosum* | potato | AG | 369 | 543 | -16 | (Conn and Cochran, 2006) |
| *Solanum tuberosum* | potato | AG | 369 | 707 | 0 | (Conn and Cochran, 2006) |
| *Beta vulgaris* | sugar beet | BG | 332 | 775 | 29 | (Ziska et al., 1995) |
| *Beta vulgaris* | sugar beet | BG | 332 | 775 | 178 | (Ziska et al., 1995) |
| *Beta vulgaris* | sugar beet | BG | 332 | 775 | 87 | (Ziska et al., 1995) |
| *Beta vulgaris* | sugar beet | BG | 375 | 550 | 14 | (Manderscheid et al., 2010) |
| *Beta vulgaris* | sugar beet | BG | 375 | 550 | 10 | (Manderscheid et al., 2010) |
| *Beta vulgaris* | sugar beet | BG | 375 | 550 | 17 | (Manderscheid et al., 2010) |
| *Beta vulgaris* | sugar beet | BG | 375 | 550 | 8 | (Manderscheid et al., 2010) |
| *Beta vulgaris* | sugar beet | BG | 375 | 550 | 36 | (Manderscheid et al., 2010) |
| *Beta vulgaris* | sugar beet | BG | 375 | 550 | 18 | (Manderscheid et al., 2010) |
| *Beta vulgaris* | sugar beet | BG | 378 | 668 | 26 | (Demmers-Derks et al., 1998) |
| *Daucus carota* | carrot | BG | 348 | 551 | 31 | (Wheeler et al., 1994) |
| *Daucus carota* | carrot | BG | 348 | 551 | 80 | (Wheeler et al., 1994) |
| *Ipomoea batatas* | sweet potato | BG | 364 | 438 | 63 | (Bhattacharya et al., 1990) |
| *Ipomoea batatas* | sweet potato | BG | 364 | 666 | 40 | (Bhattacharya et al., 1990) |
| *Ipomoea batatas* | sweet potato | BG | 361 | 438 | 26 | (Biswas et al., 1996) |
| *Ipomoea batatas* | sweet potato | BG | 361 | 514 | 43 | (Biswas et al., 1996) |
| *Ipomoea batatas* | sweet potato | BG | 361 | 665 | 69 | (Biswas et al., 1996) |
| *Raphanus sativus* | radish | BG | 350 | 650 | 70 | (Jablonski, 1997) |
| *Raphanus sativus* | radish | BG | 330 | 600 | 40 | (Chu et al., 1992) |
| *Raphanus sativus* | radish | BG | 386 | 761 | 43 | (Barnes and Pfirrmann, 1992) |
| *Raphanus sativus* | radish | BG | 350 | 700 | 289 | (Wong, 1993) |
| *Raphanus sativus* | radish | BG | 350 | 700 | 113 | (Wong, 1993) |
| *Raphanus sativus* | radish | BG | 350 | 650 | 78 | (Overdieck et al., 1988) |
| *Solanum tuberosum* | potato | BG | 360 | 460 | -5 | (Miglietta et al., 1998) |
| *Solanum tuberosum* | potato | BG | 360 | 560 | 9 | (Miglietta et al., 1998) |
| *Solanum tuberosum* | potato | BG | 360 | 660 | 4 | (Miglietta et al., 1998) |
| *Solanum tuberosum* | potato | BG | 380 | 550 | 6 | (Högy and Fangmeier, 2009) |

| Species | Common | Type[a] | Control[b] | Treatment | Value | Reference[c] |
|---|---|---|---|---|---|---|
| *Solanum tuberosum* | potato | BG | 370 | 715 | 29 | (Heagle et al., 2003) |
| *Solanum tuberosum* | potato | BG | 370 | 540 | 20 | (Heagle et al., 2003) |
| *Solanum tuberosum* | potato | BG | 370 | 715 | 22 | (Heagle et al., 2003) |
| *Solanum tuberosum* | potato | BG | ambient | 680 | 3 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | BG | ambient | 680 | 16 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | BG | ambient | 680 | 24 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | BG | ambient | 680 | 9 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | BG | ambient | 680 | 12 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | BG | ambient | 680 | 40 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | BG | ambient | 680 | 54 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | BG | ambient | 680 | -7 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | BG | ambient | 680 | 11 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | BG | ambient | 680 | 41 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | BG | 398 | 543 | 26 | (Donnelly et al., 2001) |
| *Solanum tuberosum* | potato | BG | 398 | 694 | 41 | (Donnelly et al., 2001) |
| *Solanum tuberosum* | potato | BG | 369 | 543 | 20 | (Conn and Cochran, 2006) |
| *Solanum tuberosum* | potato | BG | 369 | 707 | 36 | (Conn and Cochran, 2006) |
| *Beta vulgaris* | sugar beet | TOT | 350 | 675 | 94 | (Sionit et al., 1982) |
| *Beta vulgaris* | sugar beet | TOT | 350 | 675 | 114 | (Sionit et al., 1982) |
| *Beta vulgaris* | sugar beet | TOT | 366 | 703 | 55 | (Ziska et al., 1995) |
| *Beta vulgaris* | sugar beet | TOT | 332 | 725 | 41 | (Ziska et al., 1995) |
| *Beta vulgaris* | sugar beet | TOT | 332 | 725 | 141 | (Ziska et al., 1995) |
| *Beta vulgaris* | sugar beet | TOT | 375 | 550 | 6 | (Manderscheid et al., 2010) |
| *Beta vulgaris* | sugar beet | TOT | 375 | 550 | 8 | (Manderscheid et al., 2010) |
| *Beta vulgaris* | sugar beet | TOT | 375 | 550 | 18 | (Manderscheid et al., 2010) |
| *Beta vulgaris* | sugar beet | TOT | 375 | 550 | 7 | (Manderscheid et al., 2010) |
| *Beta vulgaris* | sugar beet | TOT | 375 | 550 | 29 | (Manderscheid et al., 2010) |
| *Beta vulgaris* | sugar beet | TOT | 375 | 550 | 19 | (Manderscheid et al., 2010) |
| *Beta vulgaris* | sugar beet | TOT | 372 | 592 | 16 | (Demmers-Derks et al., 1998) |
| *Beta vulgaris* | sugar beet | TOT | 377 | 709 | 27 | (Demmers-Derks et al., 1998) |
| *Beta vulgaris* | sugar beet | TOT | 384 | 704 | 25 | (Demmers-Derks et al., 1998) |
| *Daucus carota* | carrot | TOT | 340 | 640 | 176 | (Idso and Kimball, 1989) |
| *Daucus carota* | carrot | TOT | 348 | 551 | 16 | (Wheeler et al., 1994) |
| *Daucus carota* | carrot | TOT | 348 | 551 | 25 | (Wheeler et al., 1994) |
| *Ipomoea batatas* | sweet potato | TOT | 364 | 666 | 46 | (Bhattacharya et al., 1990) |
| *Ipomoea batatas* | sweet potato | TOT | 364 | 666 | 31 | (Bhattacharya et al., 1990) |
| *Ipomoea batatas* | sweet potato | TOT | 361 | 438 | 2 | (Biswas et al., 1996) |
| *Ipomoea batatas* | sweet potato | TOT | 361 | 514 | 17 | (Biswas et al., 1996) |
| *Ipomoea batatas* | sweet potato | TOT | 361 | 665 | 40 | (Biswas et al., 1996) |
| *Raphanus sativus* | radish | TOT | 340 | 680 | 72 | (Morison and Gifford, 1984) |
| *Raphanus sativus* | radish | TOT | 350 | 650 | 50 | (Jablonski, 1997) |
| *Raphanus sativus* | radish | TOT | 330 | 600 | 30 | (Chu et al., 1992) |
| *Raphanus sativus* | radish | TOT | 340 | 640 | 52 | (Idso and Kimball, 1989) |
| *Raphanus sativus* | radish | TOT | 350 | 675 | 63 | (Sionit et al., 1982) |
| *Raphanus sativus* | radish | TOT | 350 | 675 | 33 | (Sionit et al., 1982) |
| *Raphanus sativus* | radish | TOT | 386 | 761 | 36 | (Barnes and Pfirrmann, 1992) |
| *Raphanus sativus* | radish | TOT | 350 | 700 | 73 | (Wong, 1993) |
| *Raphanus sativus* | radish | TOT | 350 | 700 | 67 | (Wong, 1993) |
| *Raphanus sativus* | radish | TOT | 350 | 650 | 51 | (Overdieck et al., 1988) |
| *Solanum tuberosum* | potato | TOT | 380 | 550 | 5 | (Högy and Fangmeier, 2009) |
| *Solanum tuberosum* | potato | TOT | ambient | 680 | -3 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | TOT | ambient | 680 | 3 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | TOT | ambient | 680 | 18 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | TOT | ambient | 680 | 7 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | TOT | ambient | 680 | 9 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | TOT | ambient | 680 | 37 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | TOT | ambient | 680 | 39 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | TOT | ambient | 680 | 12 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | TOT | ambient | 680 | 28 | (Craigon et al., 2002) |
| *Solanum tuberosum* | potato | TOT | 398 | 543 | 25 | (Donnelly et al., 2001) |
| *Solanum tuberosum* | potato | TOT | 398 | 694 | 38 | (Donnelly et al., 2001) |

[a]AG = above ground, BG = below ground, TOT = Total

[b]ambient = $pCO_2$ level for control chamber not given.

[c]References are as follows:

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**Table S3**

Biomass data.

| Plant # | $p$CO$_2$ (ppmv) | Above ground [ln(mg)][a] | Below ground [ln(mg)][a] |
|---|---|---|---|
| 1 | 348 | 5.39 | 3.91 |
| 2 | 348 | 5.08 | 2.30 |
| 3 | 348 | 4.94 | 2.30 |
| 4 | 348 | 5.39 | 3.91 |
| 5 | 348 | 5.63 | 4.94 |
| 6 | 348 | 5.14 | 4.09 |
| 7 | 348 | 4.70 | 3.91 |
| 8 | 348 | 4.61 | 2.30 |
| 9 | 348 | 5.25 | 3.69 |
| 10 | 348 | 5.19 | 3.69 |
| 11 | 348 | 5.19 | 3.00 |
| 12 | 348 | 5.44 | 3.00 |
| 13 | 348 | 5.19 | 4.50 |
| 14 | 348 | 4.87 | 4.94 |
| 15 | 348 | 5.30 | 4.50 |
| 16 | 348 | 5.25 | 4.50 |
| *Average* | *348* | *5.19 ± 0.27* | *4.04 ± 0.90* |
| 17 | 388 | 5.52 | 3.91 |
| 18 | 388 | 5.60 | 5.19 |
| 19 | 388 | 5.25 | 5.25 |
| 20 | 388 | 4.79 | 2.30 |
| 21 | 388 | 5.39 | 5.30 |
| 22 | 388 | 5.56 | 5.30 |
| 23 | 388 | 5.70 | 4.38 |
| 24 | 388 | 5.67 | 5.14 |
| 25 | 388 | 5.35 | 3.91 |
| 26 | 388 | 5.60 | 3.91 |
| 27 | 388 | 5.56 | 2.30 |
| 28 | 388 | 4.79 | 2.30 |
| 29 | 388 | 5.01 | 3.91 |
| 30 | 388 | 3.91 | 4.09 |
| 31 | 388 | 5.48 | 2.30 |
| 32 | 388 | 5.44 | –[b] |
| *Average* | *388* | *5.37 ± 0.47* | *4.48 ± 1.18* |
| 33 | 413 | 5.46 | 5.59 |
| 34 | 413 | 5.08 | 4.32 |
| 35 | 413 | 6.07 | 5.68 |
| 36 | 413 | 5.14 | 5.13 |
| 37 | 413 | 5.46 | 5.41 |
| 38 | 413 | 5.48 | 5.07 |
| 39 | 413 | 5.79 | 4.75 |
| 40 | 413 | 5.68 | 5.39 |
| 41 | 413 | 5.03 | 2.77 |
| 42 | 413 | 5.38 | 3.18 |
| 43 | 413 | 5.23 | 4.53 |
| 44 | 413 | 5.67 | 4.91 |
| 45 | 413 | 5.73 | 5.56 |
| 46 | 413 | 5.59 | 5.24 |
| 47 | 413 | 5.98 | 4.97 |
| 48 | 413 | 5.64 | 3.67 |
| 49 | 413 | 5.43 | 3.75 |
| 50 | 413 | 5.84 | 3.46 |
| *Average* | *413* | *5.58 ± 0.30* | *4.93 ± 0.90* |
| 51 | 426 | 5.59 | 5.63 |
| 52 | 426 | 5.54 | 5.93 |
| 53 | 426 | 5.61 | 5.79 |
| 54 | 426 | 5.66 | 6.10 |
| 55 | 426 | 5.48 | 6.17 |
| 56 | 426 | 5.88 | 4.42 |
| 57 | 426 | 5.16 | 5.27 |
| 58 | 426 | 5.64 | 4.33 |
| 59 | 426 | 5.84 | 5.63 |
| 60 | 426 | 5.59 | 5.61 |
| 61 | 426 | 5.61 | 5.38 |
| 62 | 426 | 5.32 | 5.91 |
| 63 | 426 | 5.65 | 5.40 |
| 64 | 426 | 5.13 | 5.07 |
| 65 | 426 | 5.72 | 4.88 |
| 66 | 426 | 5.73 | 5.07 |
| *Average* | *426* | *5.59 ± 0.21* | *5.54 ± 0.55* |

| Plant # | $p$CO$_2$ (ppmv) | Above ground [ln(mg)] | Below ground [ln(mg)] |
|---|---|---|---|
| 67 | 760 | 5.56 | 5.80 |
| 68 | 760 | 5.77 | 6.02 |
| 69 | 760 | 5.60 | 6.11 |
| 70 | 760 | 5.83 | 6.02 |
| 71 | 760 | 6.02 | 6.13 |
| 72 | 760 | 5.67 | 5.74 |
| 73 | 760 | 6.09 | 6.13 |
| 74 | 760 | 5.60 | 5.74 |
| 75 | 760 | 5.60 | 5.60 |
| 76 | 760 | 5.52 | 4.50 |
| 77 | 760 | 5.86 | 5.08 |
| 78 | 760 | 5.80 | 5.77 |
| 79 | 760 | 5.35 | 5.52 |
| 80 | 760 | 5.56 | 4.38 |
| 81 | 760 | 6.09 | 5.35 |
| 82 | 760 | 5.60 | 5.74 |
| *Average* | *760* | *5.74 ± 0.21* | *5.71 ± 0.54* |
| 83 | 1090 | 5.67 | 5.56 |
| 84 | 1090 | 5.60 | 5.63 |
| 85 | 1090 | 5.60 | 6.29 |
| 86 | 1090 | 5.63 | 4.94 |
| 87 | 1090 | 6.04 | 5.08 |
| 88 | 1090 | 5.44 | 5.52 |
| 89 | 1090 | 5.63 | 5.83 |
| 90 | 1090 | 5.35 | 6.23 |
| 91 | 1090 | 4.94 | 4.94 |
| 92 | 1090 | 6.02 | 5.39 |
| 93 | 1090 | 6.06 | 5.35 |
| 94 | 1090 | 5.63 | 4.25 |
| 95 | 1090 | 5.67 | 5.48 |
| 96 | 1090 | 5.60 | 3.91 |
| 97 | 1090 | 5.83 | 4.38 |
| 98 | 1090 | 5.39 | 4.61 |
| *Average* | *1090* | *5.67 ± 0.28* | *5.41 ± 0.68* |
| 99 | 1425 | 6.00 | 6.48 |
| 100 | 1425 | 6.04 | 5.66 |
| 101 | 1425 | 6.13 | 6.06 |
| 102 | 1425 | 5.73 | 6.04 |
| 103 | 1425 | 5.94 | 5.76 |
| 104 | 1425 | 5.74 | 5.23 |
| 105 | 1425 | 5.81 | 5.29 |
| 106 | 1425 | 5.54 | 5.17 |
| 107 | 1425 | 5.60 | 5.09 |
| 108 | 1425 | 5.97 | 5.16 |
| 109 | 1425 | 5.91 | 5.39 |
| 110 | 1425 | 5.51 | 5.50 |
| 111 | 1425 | 5.38 | 5.59 |
| 112 | 1425 | 5.78 | 5.68 |
| 113 | 1425 | 5.99 | 5.31 |
| 114 | 1425 | 5.72 | 3.59 |
| 115 | 1425 | 5.86 | 5.24 |
| 116 | 1425 | 5.55 | 3.02 |
| *Average* | *1425* | *5.81 ± 0.21* | *5.52 ± 0.82* |
| 117 | 1791 | 5.87 | 6.20 |
| 118 | 1791 | 5.99 | – |
| 119 | 1791 | 5.90 | 6.42 |
| 120 | 1791 | 5.42 | 6.42 |
| 121 | 1791 | 5.45 | 6.07 |
| 122 | 1791 | 5.65 | 6.30 |
| 123 | 1791 | 5.65 | 6.33 |
| 124 | 1791 | 5.18 | 5.98 |
| 125 | 1791 | 5.39 | 5.50 |
| 126 | 1791 | 5.72 | 5.58 |
| 127 | 1791 | 5.84 | 6.02 |
| 128 | 1791 | 5.86 | 6.36 |
| 129 | 1791 | 5.90 | 5.77 |
| 130 | 1791 | 5.89 | 4.18 |
| 131 | 1791 | 5.74 | 6.30 |
| 132 | 1791 | 6.10 | 5.20 |
| *Average* | *1791* | *5.75 ± 0.25* | *5.87 ± 0.60* |

[a]All reported uncertainties are 1σ.

[b]No data.