Responses of *Angelica acutiloba* Kitagawa Transplants to Elevated Ambient CO₂ Concentration

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Additional index words. elevated CO₂ concentration, *Angelica*, canopy net photosynthetic rate, dark respiration rate, dry weight

Abstract. Long-term exposure to an elevated ambient carbon dioxide (eCO₂) concentration could weaken or diminish the enhancement of plant photosynthesis and growth. To monitor this response and offer references for growth management, the whole-plant photosynthetic rate ($P_{n,w}$) and dark respiration rate ($R_{d,w}$) of *Angelica acutiloba* Kitagawa transplants were monitored with a growth chamber. The results showed that eCO₂ increased both the $P_{n,w}$ and $R_{d,w}$ by (79 ± 42) % and (126 ± 51) %. The dry weight of transplants under eCO₂ was 33.6% greater than that under aCO₂. However, the photosynthetic acclimation to eCO₂ occurred. The increase in the $P_{n,w}$ was maintained until the end of the experiment due to increased leaf area. Moreover, the increase in plant dry weight mainly occurred in the first 15 days of treatment. Furthermore, the dry weight estimated based on the $P_{n,w}$ and $R_{d,w}$ agreed well with the measured dry weight. The relative growth rate (RGR) calculated with the estimated dry weight demonstrated the response of transplant growth to eCO₂. These results indicated that the proposed method can be used to monitor the response of plant growth to eCO₂.

CO₂ is the substrate for plant photosynthesis. An eCO₂ concentration can stimulate the photosynthetic rate by increasing the substrate availability of Rubisco carboxylation and inhibiting the competitive oxygenation of the enzyme (Long et al., 2004; Stitt and Krapp, 1999). As a result, plants exposed to eCO₂ usually show accelerated growth rates and high yields (e.g., Amthor 1995; Bowes, 1993; Drake et al., 1997; Poorter, 1993; Prior et al., 2003). Considering that plants grown in horticultural facilities usually are exposed to low indoor CO₂ concentrations, eCO₂ is an important technology in horticultural production (e.g., Sanchez-Guerrero et al., 2005).

The stimulation of photosynthesis by eCO₂ only increases the carbon availability of plants, and the extent to which stimulated photosynthesis can be translated into stimulated growth depends on the capability of a plant to use increased carbon under eCO₂ (Kirschbaum, 2011). Usually, plants with a large sink size or optimized nutrient supply can take advantage of eCO₂ and show stimulated photosynthetic rates and increased

biomass accumulation (Dong et al., 2017; Qian et al., 2012). However, plants with a small sink size or poor nutrient supply cannot make full use of the carbon synthesized under eCO₂ and show a small increase in biomass accumulation (Drake et al., 1997; Stitt and Krapp, 1999; Woodward, 2002). Bruggink (1984) found that a 40% to 50% increase in photosynthesis under eCO₂ of 1000 μmol·mol⁻¹ increased the RGR by only less than 15%. Yelle et al. (1990) reported that eCO₂ of 900 μmol·mol⁻¹ increased the RGR and yield of tomato plants only during the first 2 weeks of treatment. Moreover, excess synthesized carbon can remain in leaves and lead to the down-regulation of photosynthesis. Thus, it is necessary to monitor the growth of plants, especially dry weight production, under eCO₂. Then, measures of optimizing the environment or fertilization strategies can be implemented to further improve the benefits of eCO₂.

The plant dry mass can be estimated non-destructively based on the linear regression equations by inputting the easily measured parameters, such as leaf width, length, or SPAD value, etc. (Cho et al., 2007; Van Henten and Bontsema, 1995). The development of information technology further facilitates the access of those parameters and made the estimation of plant dry mass more convenient. However, the linear equation had to be validated if the growth conditions were changed (Catchpole and Wheeler, 1992; López-Díaz et al., 2011). In addition, plant dry weight production can be estimated nondestructively

by measuring the CO₂ flux from a canopy with an altered growth chamber (Bugbee, 1992; Teitel et al., 2008). Compared with the measurement of gas exchange at the leaf scale, this method can offer a continuous, long-term measurement of CO₂ flux at the canopy level (Li et al., 2012a). Most importantly, the canopy net photosynthetic rate measured with this method can be more accurate than that calculated by scaling up the leaf photosynthetic rate (Ferraz et al., 2016). This method has been applied to measure the $P_{n,w}$ of cucumber transplants (Mun et al., 2011), lettuce (Wheeler et al., 1994a), and tomato seedlings (Li et al., 2012b). Dry weight production also has been estimated based on the CO₂ flux from the canopy measured with such methods (Burkart et al., 2007; Li et al., 2012b; Wheeler et al., 1994b).

Angelica acutiloba Kitagawa (hereafter referred to as “*Angelica*”) is an important herb of which roots can be processed into a kind of traditional Chinese medicine (Lu et al., 2004). However, the growth rate of *Angelica* plants is extremely slow, and it takes 1 year to produce transplants, which limits the yield. The development of high-efficiency cultivation methods to accelerate *Angelica* growth and meet the growing market is needed urgently. In this study, adjusted growth chamber methods were used to estimate the $P_{n,w}$ and $R_{d,w}$. The purpose of this study was to examine the effects of eCO₂ on *Angelica* transplant growth. The RGR estimated with $P_{n,w}$ and $R_{d,w}$ was estimated to check the feasibility of monitoring the *Angelica* transplant growth under eCO₂. This work would be helpful for improving the response of plant growth to eCO₂.

Materials and Methods

Plant material. Seeds of *Angelica acutiloba* Kitagawa were sown in 120-well plastic trays filled with rockwool. The trays were placed in a germinating chamber with a 25 °C temperature and 80% relative humidity to accelerate germination. After 3 d of germination, the trays were moved to a growth chamber with a photoperiod of 16 h [400 μmol·m⁻²·s⁻¹ of photosynthetic photon flux density (PPFD) provided by “cool white” fluorescent lamps on the top surface of tray]. The day/night regimes of temperature and relative humidity were 25/19 °C and 70%/80%, respectively. The seedlings were irrigated daily with a nutrient solution for which the electrical conductivity was maintained at 2.0 dS·m⁻¹. High-purity CO₂ was supplied with a compressed gas cylinder to maintain the CO₂ concentration inside the growth chamber during the photoperiod at 1000 μmol·mol⁻¹.

Treatments. After 14 d of germination, *Angelica* seedlings with two expanded leaves were transplanted into a 50-well tray filled with rockwool to avoid emitting CO₂ from microorganisms into the growth chamber. Then, the transplants were transferred to two controlled-environment growth chambers

Received for publication 2 Nov. 2018. Accepted for publication 3 Feb. 2019.

This work was supported by the Fundamental Research Funds of China Agricultural University and the open projects of Key Laboratory of Protected Agriculture Engineering in the Middle and Lower Reaches of Yangtze River, Ministry of Agriculture.

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(Sanyo Gallenkamp Fitotron, Leicester, UK). The growth chamber was 0.38 m in depth, 0.6 m in length, and 0.55 m in height with a volume of 125 L. The air current speed inside the growth chamber was 0.3 m·s⁻¹. The distance from lamps to the top surface of the tray was 0.5 m. *PPFD* on the top surface of the tray was 400 μmol·m⁻²·s⁻¹. The CO₂ concentration inside the growth chambers during the photoperiod was maintained at ambient or elevated CO₂ concentration (1500 μmol·mol⁻¹) by supplying high-purity CO₂ with a compressed gas cylinder. CO₂ was not supplied during the dark period. The nutrient solution (Otsuka solution, 1/2 strength) was supplied through subirrigation every day.

Gas exchange measurement and calculations. During the experiment, the $P_{n,w}$ (μmol CO₂·h⁻¹/transplant) and $R_{d,w}$ (μmol CO₂·h⁻¹/transplant) were estimated by using the following equations.

$$P_{n,w} = \frac{N_p \cdot k \cdot V \cdot (C_{out} - C_{in}) + S}{n} \quad [1]$$

$$R_{d,w} = -\frac{N_d \cdot k \cdot V \cdot (C_{out} - C_{in})}{n} \quad [2]$$

where N_p and N_d are the numbers of air exchanges of the growth chamber during the photoperiod and dark period, respectively (h⁻¹); k is the coefficient for converting the CO₂ volume into moles (μmol·m⁻³) calculated following Campbell and Norman (1998); V is the air volume of the growth chamber (0.125·m³); C_{out} and C_{in} are the CO₂ concentrations outside and inside the growth chamber, respectively (μmol·mol⁻¹); S is the CO₂ supply rate (μmol·h⁻¹); and n is the number of transplants in the growth chamber.

In this experiment, the constant N_p and N_d were employed and may cause errors in $P_{n,w}$ and $R_{d,w}$. Then, the percent errors in N_p (e_{Np} , %), N_d (e_{Nd} , %), $P_{n,w}$ (e_P , %), and $R_{d,w}$ (e_R , %) were calculated as follows:

$$e_{Np} = \frac{N_p - N_p'}{N_p'} \cdot 100\% \quad [3]$$

$$e_{Nd} = \frac{N_d - N_d'}{N_d'} \cdot 100\% \quad [4]$$

$$e_P = \frac{P_{n,w} - P_{n,w}'}{P_{n,w}'} \cdot 100\% \quad [5]$$

$$e_R = \frac{R_{d,w} - R_{d,w}'}{R_{d,w}'} \cdot 100\% \quad [6]$$

where N_p' and N_d' are the real number of air exchanges per hour (h⁻¹) during photoperiod and dark period, respectively, and $P_{n,w}'$ and $R_{d,w}'$ are the real net photosynthetic rate and dark respiration rate of whole-plant (μmol·h⁻¹/transplant).

Substituting Eqs. [3] and [5] into Eq. [1], e_P can be calculated as:

$$e_P = \frac{N_p' \cdot K \cdot V \cdot (C_{out} - C_{in})}{P_{n,w}'} \cdot e_N \quad [7]$$

Substituting Eqs. [4] and [6] into Eq. [2], e_R can be calculated as:

$$e_R = -\frac{N_d' \cdot K \cdot V \cdot (C_{out} - C_{in})}{R_{d,w}'} \cdot e_N \quad [8]$$

The dry weight accumulation of the transplants in 'u' days ($W_{E,u}$, g/transplant) was estimated as follows:

$$W_{E,u} = W_0 + m \cdot j \cdot \sum_{i=0}^u (L_p \cdot P_{n,w,i} - L_d \cdot R_{d,w,i}) \quad [9]$$

where W_0 is the initial dry weight of the transplants (g/transplant), m is the coefficient for converting moles of CO₂ into mass (44×10^{-6} g·μmol⁻¹), j is the coefficient for converting the CO₂ assimilated by transplants into dry weight (0.68 g·g⁻¹; Van Henten, 1994), L_p and L_d are the lengths of the light period and dark period, respectively (h·d⁻¹), and $P_{n,w,i}$ and $R_{d,w,i}$ are the average estimated $P_{n,w}$ and $R_{d,w}$ on day 'i', respectively.

The *RGR* of transplants on day 'u' ($RGR_{E,u}$, g·g⁻¹) was estimated as follows:

$$RGR_{E,u} = \ln(W_{E,u}) - \ln(W_{E,u-1}) \quad [10]$$

Measurements. CO₂ concentrations inside and outside the growth chamber were measured using an infrared gas analyzer (GMP 222; Vaisala Oyj, Helsinki, Finland; precision: ± 15 μmol·mol⁻¹). The sensors inside the growth chamber were located at the center of the interior space at the same height as that of the sensors located outside. Hourly averaged data were recorded and used to estimate $P_{n,w}$ and $R_{d,w}$. The CO₂ concentrations were measured every 10 min and averaged per hour automatically. The CO₂ injection rate was adjusted manually by adjusting the knob of the air pump in the first 2 h of photoperiod to maintain the target CO₂ concentration inside the growth chamber. After then, the CO₂ was injected into the growth chamber at a constant rate and the accumulated amount of injected CO₂ was recorded with a flow meter (TC-1000-200; Tokyo Keiso Corp., Japan). The CO₂ injection rate was calculated as the ratio of the accumulated CO₂ amount injected into growth chamber with time. The data collected during the first 2 h after both the dark–light transition and the light–dark transition were discarded to ensure that the environmental conditions were stable.

Both N_p and N_d were measured in the absence of plants and calculated following Li et al. (2012b). Every 5 d, five transplants were sampled from each treatment to measure the leaf area and dry weight. The leaves of the sampled transplants were scanned with digital cameras, and the area was measured with image analysis software (LIA for Win32, freely available from <http://www.agr.nagoya-u.ac.jp/%7Eshinkan/LIA32/index>). Then, the whole plants were dried at 60 °C for 1 week to determine the dry weight with an electronic balance (PL303, precision: ± 0.001 g; Mettler–Toledo, Greifensee, Switzerland). The significant difference in dry weight data were analyzed using analysis of variance at $P < 0.05$ with Student's *t* test in SPSS 22.0 (IBM Corp., Armonk, NY).

At the end of the experiment, three transplants from each treatment were selected to measure the CO₂ assimilation rate of their third leaf (counting from the bottom) using a portable photosynthesis system (LI-6400; LI-COR, Inc., Lincoln, NE). At the inlet of the leaf chamber, the CO₂ concentration was set at 200, 250, 300, 400, 600, 800, 1000, or 1200 μmol·mol⁻¹. The *PPFD* and air temperature were maintained at 400 μmol·m⁻²·s⁻¹ and 25 °C, respectively. The measurements were repeated three times.

Results

The CO₂ injection rate and CO₂ concentrations inside and outside growth chamber are shown in Fig. 1. The CO₂ concentrations inside growth chambers with eCO₂ and aCO₂ during photoperiod were maintained at 1523 ± 23 μmol·mol⁻¹ and 313 ± 23 μmol·mol⁻¹ throughout the experiment, respectively. The number of transplants inside the growth chamber is shown in Fig. 2. For one growth chamber, the number of air exchanges during photoperiod (N_p) and dark period (N_d) were 5.73 h⁻¹ and 2.31 h⁻¹, respectively. N_p and N_d of another growth chamber were 1.52 h⁻¹ and 0.89 h⁻¹, respectively. In contrast, *PPFD* on the top of transplants increased with the increase in transplant height. However, the difference in *PPFD* between the transplants under eCO₂ and aCO₂ was less than 10 μmol·m⁻²·s⁻¹. Hence, the effects of this difference on transplant growth can be neglected.

To test the accuracy of the method used to measure the $P_{n,w}$ and $R_{d,w}$, the estimated transplant dry weight (W_E) was plotted against the measured dry weight (W_M) (Fig. 3). The linear equation of W_E and W_M for transplants under eCO₂ was $W_M = 0.92 \cdot W_E$ with an r^2 value

Fig. 1. CO₂ injection rate and CO₂ concentrations inside and outside the growth chamber during the photoperiod (A) and dark period (B). Data represent the mean $\pm$ SD. CO₂ = carbon dioxide.

Fig. 2. Number of Angelica transplants inside the growth chamber.

of 0.96 ($P > 0.05$), whereas it was $W_M = 0.95 \cdot W_E$ with an r^2 value of 0.91 for transplants under aCO_2 ($P > 0.05$). The largest differences between W_M and W_E were less than 12%. Thus, the measured $P_{n,w}$ and $R_{d,w}$ were accurate and could be employed to monitor the response of transplant dry weight to eCO_2 .

During the experiments, the $P_{n,w}$ and $R_{n,w}$ of transplants grown under either eCO_2 or aCO_2 increased with time (Figs. 4 and 5). The ratios of $R_{n,w}$ to $P_{n,w}$ of the transplants under eCO_2 and aCO_2 were $(74 \pm 12)\%$ and $(60 \pm 16)\%$ during the experiment. Finally, the CO_2 released by transplants under eCO_2 and aCO_2 during dark period were $(37 \pm 6)\%$ and $(30 \pm 8)\%$ of those fixed during photoperiod, respectively. In contrast, both $P_{n,w}$ and $R_{n,w}$ were greater under eCO_2 than under aCO_2 . During the experiment, the increases in both $P_{n,w}$ and $R_{n,w}$ were $(13.9 \pm 3.9) \mu\text{mol } CO_2 \cdot h^{-1} \cdot \text{transplant}^{-1}$ and $(13.8 \pm 4.2) \mu\text{mol } CO_2 \cdot h^{-1} \cdot \text{transplant}^{-1}$, respectively. However, these increases already had occurred at the beginning of treatment and lasted until the end of the experiment. As a result, the increased ratios of the $P_{n,w}$ and $R_{n,w}$ were $(79 \pm 42)\%$ and $(126 \pm 51)\%$ greater under eCO_2 than that under aCO_2 .

At the end of the experiment, the responses of the leaf net photosynthetic rate (P_l) to different CO_2 concentrations were measured and are shown in Fig. 6. After 25 d of treatment, P_l of transplants grown under eCO_2 was lower than that of transplants grown under aCO_2 ; when the third leaf of transplants was exposed to the same CO_2 concentration, it ranged from 50 to $1200 \mu\text{mol} \cdot \text{mol}^{-1}$. Both the CO_2 compensation and saturation points of the transplants under eCO_2 decreased. This result suggests that the photosynthesis of transplants under eCO_2 acclimated to the eCO_2 by the end of the experiments (Hao et al., 2006). In addition, P_l in each day was calculated as the ratio of $P_{n,w}$ to leaf area and is shown in Fig. 7. The results showed that the initial enhancement of P_l under eCO_2 weakened with exposure time and diminished in the last few days of the experiment. Together with the phenomenon of photosynthetic acclimation observed in the transplants under eCO_2 , this result suggested that the photosynthetic capacity of transplant leaves under eCO_2 decreased.

The leaf area of the transplants under eCO_2 and aCO_2 increased exponentially with

Fig. 3. Dry weight accumulation of Angelica transplants estimated based on the whole-plant net photosynthetic rate and dark respiration rate (W_E) plotted against the measured dry weight (W_M). Data represent the mean $\pm$ SD.

Fig. 4. Whole-plant net photosynthetic rate of Angelica transplants ($P_{n,w}$) grown under elevated carbon dioxide (eCO_2) and ambient carbon dioxide (aCO_2) concentrations.

Fig. 5. Whole-plant dark respiration rate of Angelica transplants ($R_{d,w}$) grown under elevated carbon dioxide (eCO_2) and ambient carbon dioxide (aCO_2) concentrations.

time (Fig. 8). eCO_2 stimulated the extension of transplant leaves. In the first 15 d of treatment, the differences in leaf area between the transplants under eCO_2 and those under aCO_2 increased with treatment time and reached $0.0012 \text{ m}^2 \cdot \text{transplant}^{-1}$ after 15 d of treatment. However, the differences were not further enlarged with the treatment time and became $0.0015 \text{ m}^2 \cdot \text{transplant}^{-1}$. Thus, the stimulation of leaf area by eCO_2 mainly occurred during the first 15 d of treatment.

The dry weights of transplants under eCO_2 ($W_{m,e}$) and aCO_2 ($W_{m,a}$) increased with time. $W_{m,e}$ was always greater than $W_{m,a}$ through the experiment. At the end of the

Fig. 6. Response of net photosynthetic rate of Angelica transplants (P_l) grown under elevated carbon dioxide (eCO_2) and ambient carbon dioxide (aCO_2) concentrations to different CO_2 concentrations at the end of experiment. Data represent the mean $\pm$ SD.

Fig. 7. Estimated net photosynthetic rate of Angelica transplants per leaf area (P_l) under Data represent the mean $\pm$ SD.

Fig. 8. Leaf area of Angelica transplants grown under elevated carbon dioxide (eCO_2) and ambient carbon dioxide (aCO_2) concentrations. Data represent the mean $\pm$ SD.

experiment, $W_{m,e}$ was 33.6% greater than $W_{m,a}$ (Fig. 9). Nevertheless, $(W_{m,e} - W_{m,a})$ after 15 d of treatment was 81% of that at the end of the experiment. Thus, the enhancement of eCO_2 on dry weights was mainly formed in the first 15 d of treatment.

Based on W_E , the RGR was calculated (Fig. 10). The initial increase in RGR decreased with exposure time and almost diminished in the last dozen days of the experiment. Thus, both the initial increases in leaf area and dry weight accumulation mainly occurred in the first 15 d of treatment. These results coincide with those of Yelle (1990). Hence, the change in plant responses to eCO_2 can be detected with these methods.

Fig. 9. Dry weight accumulation of Angelica transplants grown under elevated carbon dioxide (eCO₂) and ambient carbon dioxide (aCO₂). (* and NS indicate significant differences at $P < 0.05$ and nonsignificant differences, respectively.) Data represent the mean $\pm$ SD.

Fig. 10. Relative growth rate (RGR) of Angelica transplants calculated based on the estimated dry weight of the transplants grown. Data represent the mean $\pm$ SD.

Discussion

The growth chamber method has been widely applied to measure the $P_{n,w}$ and $R_{d,w}$. To prevent the inaccuracy of measured $P_{n,w}$ and $R_{d,w}$, all of the concentration sensors were calibrated with standard gases in advance. The pure CO₂ was injected into the chamber at a constant rate, which was calculated with the accumulated amount of CO₂ injected into the chamber during photoperiod. This method had been calibrated by draining water from a measuring cylinder with pure nitrogen. Thus, the error caused by the CO₂ injection speed can be neglected. Then, the over- or underestimated $P_{n,w}$ and $R_{d,w}$ may be aroused by the number of air exchanges according to Eqs. [1] and [2].

The percent errors in $P_{n,w}$ (e_P) and $R_{d,w}$ (e_R) caused by the percent errors in number of air exchanges during photoperiod and dark period can be evaluated with Eqs. [7] and [8]. e_P and e_R are in proportion to e_{N_p} and e_{N_d} , respectively. It is possible to prevent and cause over- or underestimated $P_{n,w}$ and $R_{d,w}$ by diminishing the variation of N_p and N_d , which may change with the room temperature (Li et al., 2012b). In this experiment, the air conditioner had been operated continuously to maintain the room temperature, even though the room temperature changed sometimes due to the operation of other equipment or human activities and enlarged e_P and e_R .

However, the good agreement of W_E and W_M indicates that the measured $P_{n,w}$ and $R_{d,w}$ were highly accurate. They can be applied for further analysis.

Photosynthesis is well known to increase under eCO₂. However, this enhancement is not sustainable after long-term exposure to eCO₂, a phenomenon that frequently is referred to as photosynthetic acclimation or down-regulation (e.g., Ainsworth and Rogers, 2007). The angelica transplants under eCO₂ also showed this phenomenon. This phenomenon normally occurs in response to excess nonconstructive carbohydrates due to limited sink size or poor nutrient supply. In contrast, plants with a large sink size or sufficient nutrient supply can avoid this phenomenon and maintain a high photosynthetic capacity (Dong et al., 2017; Qian et al., 2012).

There are fewer reports on the response of $P_{n,w}$ to eCO₂. According to the results presented here, the variation in $P_{n,w}$ differs from that in P_l . The initial increase in $P_{n,w}$ due to eCO₂ was maintained until the end of the experiment because the leaf area of the transplants increased in response to eCO₂ and thus offset the impacts of P_l on $P_{n,w}$. However, the transplants in the experiment were young, with a leaf area index ranging from 1.3 to 3.4. A further increase in leaf area would intensify shading and no longer increase the canopy photosynthetic rate. Then, the positive effect of eCO₂ on the canopy photosynthetic rate may be further weakened.

Leaf area plays an important role in plant growth and the photosynthetic rate. Wheeler et al. (2015) observed that the onion under eCO₂ of 532 $\mu\text{mol}\cdot\text{mol}^{-1}$ showed a greater leaf area than those grown under aCO₂ of 374 $\mu\text{mol}\cdot\text{mol}^{-1}$. The results of this experiment coincide with those results. However, some reports have observed negative or neutral effects of eCO₂ on leaf area, which result from differences in growth conditions and plant species (Rachel and Gail, 2010; Usuda, 2004).

Dark respiration is a major determinant of plant dry weight accumulation, as it can return as much as 24%–50% of photosynthetically fixed carbon to the atmosphere (Amthor, 1995; Yokoi et al., 2005). However, the effects of eCO₂ on the $R_{d,w}$ vary according to plant species and growth conditions. eCO₂ reportedly can stimulate dark respiration by increasing carbohydrates or intensifying maintenance and growth respiration (Li et al., 2013; Thomas and Griffin, 1994). In this study, the $R_{d,w}$ of Angelica transplants under eCO₂ was intensified as the result of increased carbohydrates and enhanced growth.

The increase in biomass accumulation caused by eCO₂ also depends on the plant sink size or nutrient supply (Kirschbaum, 2011). Only if the plants can make full use of the increased photosynthetically synthesized carbon can their dry weights respond strongly to eCO₂. In this experiment, the plants were still young and had not yet developed large roots to consume the artificially increased carbon. In addition, the nutrient supply was not adjusted

to meet the increased requirements of transplants under eCO₂. Thus, the enhancement of the biomass of Angelica transplants caused by eCO₂ weakened with exposure time and diminished after 15 d of treatment. It is important to detect the response of plant growth to eCO₂ and take measures as soon as possible to maintain the strong response of plant growth to eCO₂.

Conclusions

In conclusion, the $P_{n,w}$ and $R_{d,w}$ were monitored with altered growth chambers. W_E of Angelica transplants grown under eCO₂ and aCO₂ agreed well with the W_M . According to the results, eCO₂ increased both the $P_{n,w}$ and $R_{d,w}$ but induced photosynthetic acclimation at the end of the experiment. The increase in $P_{n,w}$ under eCO₂ was maintained over the experiment due to increased leaf area. In addition, the increase in transplant dry weight under eCO₂ mainly occurred in the first 15 d of treatment. This phenomenon could be detected by the RGR calculated based on the W_E . These results indicated that this method can be used to monitor the dry weight accumulation of Angelica transplants under eCO₂.

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