Effects of Growth under Elevated CO₂ on the Capacity of Photosynthesis in Two Radish Cultivars Differing in Capacity of Storage Root

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Abstract: The effect of growth under elevated CO₂ on the capacity of photosynthesis was assessed in two cultivars of radish, *Raphanus sativus* L. cv White Cherrish and Kosena, with a large and small storage root, respectively. Plants were grown under ambient (ca. 350 μmol CO₂ mol⁻¹) and elevated (ca. 750 μmol CO₂ mol⁻¹) CO₂ and the first leaf of the plants at various ages, were examined for chlorophyll fluorescence, the maximum photosynthetic rates under saturated CO₂ (photosynthetic capacity) and the rates of transpiration simultaneously. Elevated CO₂ did not significantly reduce the capacity of photosynthesis, transpiration, quantum yield of electron transport from photosystem II (ΦPSII), and the maximum intrinsic yield of photosystem II at any developmental stage in both cultivars. In other words, growth under elevated CO₂ had no effect on the capacity of photosynthesis in either cultivar. These results suggested that not only the storage root but also vigorously growing young leaves play an important role as a sink in utilizing increased photosynthate under elevated CO₂. The elevated CO₂ accelerated ontogeny and caused a slightly earlier decline in the capacity of photosynthesis. The capacity of carbon metabolism and the photochemical capacity decreased coordinately with advancing age accompanied with the decline of photosynthetic activity under both ambient and elevated CO₂.

Key words: Aging, Chlorophyll fluorescence, CO₂ fixation, Elevated CO₂, Radish, Source-sink.

The atmospheric concentration of CO₂ will likely rise from its present level of about 350 μmol mol⁻¹ to about 700 μmol mol⁻¹ by the end of this century (Watson et al., 1990). Researches in the last several decades have demonstrated that atmospheric CO₂ enrichment tends to cause significant increases in the growth rates and yields of the most agricultural species (see, e.g., Kimball, 1983; Kimball et al., 2002). The contribution of photosynthesis to this increase, however, is unclear. CO₂ enrichment may also increase water use efficiency (see, e.g., Wullschleger et al., 2002) and has complicated effects on the photosynthetic fixation of CO₂, as discussed below. The present concentration of CO₂ in the atmosphere, 350 μmol mol⁻¹, imposes a limit to photosynthesis of C3 plants (see, e.g., Bowes, 1991; Long and Drake, 1992). Elevation of the concentration of CO₂, therefore, is expected to increase the net photosynthetic rate in C3 plants. Many studies, however, have shown that short-term gain may be offset, in the longer term, by a down regulation of photosynthetic capacity. There are two mechanisms for the down regulation of photosynthesis by elevated CO₂, which are not necessarily mutually exclusive. One is the down regulation of the expression of the photosynthetic genes caused by over accumulated sugars in source leaves (see Sheen, 1990; Stitt, 1991; Koch, 1996), and the other is the acceleration of ontogeny and early initiation of senescence (Miller et al., 1997; Usuda and Shimogawara, 1998; Kauder et al., 2000; Ludewig and Sonnewald, 2000). It is important to consider that the rate of photosynthesis is highly dependent on developmental stages and the response to CO₂ varies with the stage of development (e.g. Nie et al., 1995; van Oosten and Besford, 1995; van Oosten et al., 1995; Pearson and Brooks, 1995; Usuda and Shimogawara, 1998). For this reason, I examined the photosynthetic capacity of the first leaf of plants at various developmental stages under ambient and elevated CO₂.

Utilization of photosynthate is highly dependent on the capacity of sink. Therefore, the elucidation of the effect of sink capacity on the acclimation of...
photosynthesis to elevated CO$_2$ during plant growth is also very important. We previously studied the radish cultivar, White Cherrish (WC) which has a large storage root. Under CO$_2$ enrichment there was no over-accumulation of carbohydrates in source leaves and we suggested the absence of the down regulation of photosynthetic capacity caused by the first mechanism (feedback by sugar accumulation). The ontogeny was, however, accelerated under elevated CO$_2$ (Usuda and Shimogawara, 1998). We also compared the effects of growth under elevated CO$_2$ on the capacity of photosynthesis and growth in another cultivar, Kosena (K) which has a smaller storage root like the wild radish, with those in WC (Usuda and Rouhier, 2001). The dry weights (DWs) of storage root were about 50% and 3% of total dry weights in WC and K, respectively (Usuda et al., 1999a; Usuda et al., 1999b). We measured the rate of photosynthesis using 2- and 3-week old K plants grown under ambient and elevated CO$_2$ and found that the rates with elevated CO$_2$ grown plants were similar or slightly lower than those of plants grown under ambient CO$_2$ (Usuda and Rouhier, 2001). However, the effects of growth under elevated CO$_2$ on the capacity of photosynthesis in K were inconclusive, because the rate of photosynthesis changes greatly during development (see, e.g., Usuda and Shimogawara, 1998). Therefore this study was carried out to study photosynthesis throughout development in order to clarify the effect of storage root as a sink on the regulation of the capacity of photosynthesis under elevated CO$_2$ using two cultivars differing in capacity of storage root. The CO$_2$ saturated rates of photosynthesis and chlorophyll fluorescence were measured simultaneously almost every two days from 11 to 29 days after planting (DAP) to evaluate the effects of growth under elevated CO$_2$ on the photosynthetic capacity precisely.

Material and Methods

1. Plant material and growth conditions

Seeds of radish, *Raphanus sativus* L. cv White Cherrish (WC) and cv Kosena (K) were obtained from Sakata Seed Co. (Yokohama, Japan) and Watanabe-Saishujo (Miyagi, Japan), respectively. Seeds were incubated on moist filter paper in darkness for 3 days at 25±1°C and the seedlings were transferred to hydroponic culture (for the composition of culture medium, see Usuda et al., 1999a). They were grown under a 14.5-h light/9.5-h dark cycle with a day/night temperature of 25±1/21±1°C in a walk-in type controlled growth chamber (Akitsu-keisoku, Tokyo, Japan). The photon irradiance at plant height was increased gradually to ca. 440 from 0 µmol m$^{-2}$ s$^{-1}$ during the first 30 min of light period with metal-halide lamps (MLBOC400C-U, Mitsubishi Electric, Tokyo, Japan), ca. 550 µmol m$^{-2}$ s$^{-1}$ for 13.5 h with metal-halide and fluorescent lamps (FPR96EX, Matsushita Electric, Osaka, Japan) and 440 µmol m$^{-2}$ s$^{-1}$ during the last 30 min of the light period with metal-halide lamps. The concentration of CO$_2$ in the chamber was monitored with a CO$_2$ controller (ZFP 9; Fuji Electric Co., Tokyo, Japan) and maintained at 350 ± 20 (ambient CO$_2$) or 750 ± 20 µm mol$^{-1}$ (elevated CO$_2$) with a CO$_2$ injection and absorption system. At 9 DAP, nine relatively uniform plants were selected, and each plant was cultured in a container with ca. 5.5 L of aerated culture solution. All containers were rotated 6 times a week to reduce the effects of heterogeneity of the conditions within the growth chamber.

2. Determination of CO$_2$ exchange and chlorophyll fluorescence in the first leaf of plants at various ages

The rates of CO$_2$ exchange and transpiration, and chlorophyll fluorescence in the first leaf of 11- to 29-day-old plants were determined simultaneously with an open system using an infrared gas analyzer (LI-6400 equipped with a leaf chamber fluorometer, LI-COR, Lincoln, USA). The middle part of the first leaf (2 cm$^2$) was used for the measurements. Measurements were conducted in the growth chamber to reduce the artificial effects on the plant as much as possible from ca. 4 hrs after the onset of irradiation to ca. 4 hrs before the cessation of irradiation. Leaf temperature was kept at 25±0.5°C. Relative humidity in the leaf chamber was around 50 to 75%. The rates of CO$_2$ exchange and transpiration, and chlorophyll fluorescence were monitored under the following five conditions successively. For CO$_2$ concentration, the values for the inlet air are mostly shown here. The maximum difference in CO$_2$ concentration between the inlet and the outlet air was about 80 µmol mol$^{-1}$ when the rate of photosynthesis was about 57 µmol mol$^{-1}$ CO$_2$ m$^{-2}$ s$^{-1}$. The sequence of measurements were: 1) Exposure to actinic light at 1,200 µmol photons m$^{-2}$ s$^{-1}$ with 170 µmol mol$^{-1}$ CO$_2$ for 20-30 min. 2) Exposure to actinic light intensity at 1,200 µmol photons m$^{-2}$ s$^{-1}$ with 350 µmol mol$^{-1}$ CO$_2$ for several min. 3) Exposure to actinic light intensity at 1,200 µmol photons m$^{-2}$ s$^{-1}$ with 1,000 µmol mol$^{-1}$ CO$_2$ for several min. The rate of photosynthesis measured under this condition was taken as the maximum rate of photosynthetic CO$_2$ assimilation (P$_{max}$). P$_{max}$ was corrected for dark respiration (see below) and calculated to the maximum rates of gross photosynthetic CO$_2$ assimilation (P$_{gmax}$). 4) Reduction of the actinic light intensity to 100 µmol photons m$^{-2}$ s$^{-1}$ with 400 µmol mol$^{-1}$ CO$_2$ for several min. 5) Turning off the actinic light and keeping the leaf segment under the same concentration of CO$_2$ for more than 20 min. The rate of dark respiration was high immediately after irradiation and then decreased to a steady level. This steady rate of respiration during 15 to 20 min in darkness was regarded as the rate of dark respiration (R$_d$) and it was approximated as the
rate of respiration in the light from processes other than photorespiration. Chlorophyll fluorescence was measured using a modulated fluorometer. The steady state fluorescence ($F_0$) was monitored continuously and a 600-ms pulse of saturating light of ca 7,500 μmol m$^{-2}$ s$^{-1}$ and 1,000 μmol mol$^{-1}$ CO$_2$ with short dark pulses when needed. $F_o$ and $F_m$ were measured with dark adapted leaves under 400 μmol mol$^{-1}$ CO$_2$. See the text for details. Significant differences between means were indicated by **P<0.01, *P<0.05; no mark, not significant after t-test.

fluorescence ($F'_v$) in light-adapted leaves which had momentarily been darkened with a 2-s pulse of far red light, were also determined. Far-red light was turned on for 1 s with actinic light and for another second in the dark. The light intensity of far red light was ca. 4 μmol m$^{-2}$ s$^{-1}$ and the duration of the dark period was 4.8 s. Partial pressures of CO$_2$ in the intercellular spaces of leaves ($C_i$) were obtained by a LI-6400 system which is based on the method of von Caemmerer and Farquhar (1981). Net CO$_2$ assimilation rate ($A$) versus
Ci curves, i.e. \( A-C_i \) curves were constructed at a light intensity of 1,200 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) using the same system as described above.

### 3. Computation

The chlorophyll fluorescence measurements were analyzed as originally described by Genty et al. (1989) to provide a quantum yield of electron transport from photosystem II, \( \Phi_{\text{PSII}} \) \( (F_m'-F_s)/F_m' \), photochemical quenching coefficient, \( qP \) \( (F_m'-F_o)/F_m' \), the efficiency with which absorbed quanta are transferred to the open PSII reaction centers, \( F_v'/F_m' \) \( (F_m'-F_o')/F_m' \), non-photochemical quenching coefficient, \( qN \) \( 1-(F_m'-F_o')/(F_m-F_o') \), and maximum intrinsic quantum yield of PSII, \( F_v/F_m \) \( (F_m-F_o)/F_m \). Rates of total electron transport \( (\mu \text{mol m}^{-2} \text{s}^{-1}) \) were calculated by \( J_e=aj\Phi_{\text{PSII}} \). Where \( a \) is the absorbance of leaf (0.85 was assumed), \( f \) is the fraction of absorbed quanta that is used by PSII (0.5 was assumed) and \( I \) is the incident irradiance. Rates of electron transport used for photosynthetic CO2 fixation, \( J_r \) \( (\mu \text{mol m}^{-2} \text{s}^{-1}) \), were calculated by \( J_r=4(P_{\text{max}}+R_d) \). Where \( P_{\text{max}} \) and \( R_d \) were the rates of maximum photosynthesis and dark respiration, respectively, see above. Quantum yields of photosynthetic CO2 assimilation \( (\Phi_{\text{CO2}}) \) were calculated by \( \Phi_{\text{CO2}}= (P_{\text{max}}+R_d)/al \). For \( a \) and \( I \), see above.

### 4. Statistics

For the data analyses t-tests and analyses of variance in two regression lines were done using Excel 2001 (Microsoft Corporation, Redmond, USA) and Multivariate Analysis Ver.4.0 (Esumi, Tokyo, Japan), respectively.

#### Results

1. **Enhancement of growth by elevated CO2**

   Fresh weights (FWs) of K at 25 DAP in ambient- and elevated-CO2-grown plants were 145.9±16.9 and 230.3±69.6 g plant\(^{-1}\) (mean±SD, \( n=6 \)), respectively. FWs of WC at 29 DAP in ambient- and elevated-CO2-grown plants were 194.5±25.3 and 262.7±48.6 g plant\(^{-1}\) (mean±SD, \( n=6 \)), respectively. Thus, elevated CO2 enhanced growth of K and WC by 1.58 and 1.35 folds, respectively. These enhancements of growth by elevated CO2 with two cultivars were similar to previous observations (Usuda and Rouhier, 2001). The DWs of storage root were about 50% and 3% of total DW with WC and K, respectively. The changes in the allocation of DW into shoots and root during development were described in detail previously (Usuda et al., 1999a; Usuda et al., 1999b). The date when the length of the 10th leaf became longer than 1 cm was recorded as the date of appearance of the 10th leaf. The 10th leaves of K grown under ambient and elevated CO2 appeared on 22.0±0.4 and 20.5±0.7 DAP (mean±SD, \( n=6, p<0.05 \)), respectively. The 10th leaves of WC grown under ambient and elevated CO2 appeared on 26.5±4.7 and 23.5±4.3 DAP (mean±SD, \( n=6, p<0.05 \)), respectively. These results confirmed that elevated CO2 accelerated ontogeny (Usuda and Shimogawara, 1998).

![Fig. 3. The relationship between the initial slopes of A-Ci curve and the maximum photosynthetic carbon assimilation (Pmax) in the first leaf at various ages of Kosena (a) and White Cherrish (b) grown under ambient (O) and elevated (x) CO2. Pmax and A-Ci curves were obtained under 1,200 \( \mu \text{mol photon m}^{-2} \text{s}^{-1} \). Typical original data of A-Ci curves in Kosena grown under ambient CO2 were inserted (a). Level of significance between two regression lines; NS, not significant. Correlation coefficients (R) of each line were shown. The significance of these regression lines were p<0.01. n=12 (a, O), 11 (a, x), 22 (b, O), 18 (b, x).](image-url)
2. Changes in the rates of $P_{\text{max}}$, dark respiration and transpiration and $\Phi_{\text{PSII}}$, $qP$, $F'_v/F'_m$, $F_v/F_m$ and $qN$ during development

The changes in $P_{\text{max}}$, $R_d$, transpiration rate, $\Phi_{\text{PSII}}$, $qP$, $F'_v/F'_m$, $F_v/F_m$ and $qN$ during development with ambient and elevated CO$_2$ grown K and WC were shown in Fig. 1 and 2, respectively. There was no effect of growth under elevated CO$_2$ on the maximum rate of $P_{\text{max}}$ with either K or WC (Fig. 1a, 2a). The maximum values of $P_{\text{max}}$ with elevated CO$_2$ grown plants decreased slightly faster than that of ambient CO$_2$ grown plants during development (Fig. 1a, 2a). All of these values changed greatly during the development, although $F'_v/F'_m$ showed a high value throughout the developmental period except at 25 DAP in K. The effects of elevated CO$_2$ on these values were small, but elevated CO$_2$ accelerated the decreases in these values slightly with advancing age (e.g. $P_{\text{max}}$, $\Phi_{\text{PSII}}$ and $qP$). One exception is that $qN$ in WC was slightly promoted by elevated CO$_2$ during the early phase of development (12 DAP) but not during the later stage (Fig. 2h).

3. Effect of growth under elevated CO$_2$ on the initial slope of $A_C$ curve

To assess the effect of growth under elevated CO$_2$ on the activity of ribulose 1,5-bisphosphate carboxylase in situ, the initial slopes of $A_C$ curves were compared in the first leaf of K and WC grown under ambient and elevated CO$_2$. $P_{\text{max}}$ changed during development (Fig. 1a, 2a), therefore $A_C$ curves were obtained in the first leaf of plants at various ages. A few typical examples are shown in an inserted figure in Fig. 3. The initial slopes of $A_C$ curves thus obtained were plotted against $P_{\text{max}}$. With decreasing $P_{\text{max}}$, the slopes also decreased (Fig. 3). There was no effect of growth under elevated CO$_2$ on this relationship in either K or WC (Fig. 3).

4. Relationship between $\Phi_{\text{CO}_2}$ and efficiency of utilization of light energy

The rate of photosynthetic fixation of CO$_2$, dark respiration, transpiration, $\Phi_{\text{PSII}}$, $qP$, $F'_v/F'_m$, and $qN$ in the first leaf of K and WC grown under ambient and elevated CO$_2$. These values were, however, affected by the growth under elevated CO$_2$ only slightly (Fig. 1, 2). The significant differences in these values seemed to be due to the change in developmental stages caused by elevated CO$_2$. Namely it is probably due to the decrease in the

![Fig. 4. Correlation of $\Phi_{\text{CO}}$ with $J_{\text{c}}/J_{\text{f}}$, $\Phi_{\text{PSII}}$, $qP$, $F'_v/F'_m$, $F_v/F_m$ and $qN$ in the first leaf at various ages in Kosena (a-c) and White Cherrish (f-j) grown under ambient (O) and elevated (±) CO$_2$. $J_c$ was the rate of electron transport used for CO$_2$ assimilation and $J_f$ was the rate of total electron transport calculated from chlorophyll fluorescence measurements. These values were obtained under 1,200 µmol photon m$^{-2}$ s$^{-1}$ and 1,000 µmol mol$^{-1}$ CO$_2$ with short dark pulses when needed. See the text for details. Levels of significance between two regression lines were shown with NS (not significant) and p<0.05. Correlation coefficients (R) of each line were shown. The significance of these lines were p<0.01. n=42 (a-c), 48 (f-j). The equations of the regression line between $\Phi_{\text{CO}_2}$ and $\Phi_{\text{PSII}}$ were, y=8.66x +0.033, y=8.81x+0.027, y=7.70x+0.081 and y=8.19x+0.054 in Kosena grown under ambient CO$_2$ (b, O), Kosena grown under elevated CO$_2$ (b, ±), White Cherrish grown under ambient CO$_2$ (g, O) and White Cherrish grown under elevated CO$_2$ (g, ±), respectively.](image-url)
capacity of photosynthesis during aging or senescence under elevated CO₂. To assess 1) the changes in the capacities of photosynthetic fixation of CO₂ and utilization of light energy during aging or senescence and 2) the effect of growth under elevated CO₂ on these changes, the relationships between ΦCO₂ and the fraction of electron transport used for CO₂ fixation, ΦPSII, qP, Fv'/Fm' and qN were analyzed. These values were obtained under the condition of 1,200 μmol photon m⁻² s⁻¹ and 1,000 μmol mol⁻¹ CO₂ in the inlet air containing 21% O₂. Under this condition the rate of photosynthesis was almost saturated (see the inserted figure in Fig. 3), therefore, the condition used to obtain ΦCO₂ in this study was referred to as a low-photorespiratory condition. This was also supported by the results that fractions of Jc against Jf were quite high in most cases except for some results obtained with very old leaves (Fig. 4a, f). There were significant positive relationships between ΦCO₂ and ΦPSII (Fig. 4b, g), qP (Fig. 4c, h), and Fv'/Fm' (Fig. 4d, i). There was a significant negative relationship between ΦCO₂ and qN (Fig. 4e, j). However, significant effects of growth under elevated CO₂ on these relationships were not observed except one, the relationship between ΦCO₂ and qN in K.

5. Relationship between Fv'/Fm' and qN

To assess the mechanisms underlying in the changes in the value of Fv'/Fm', the relationship between Fv'/Fm' and qN were plotted using the data shown above. There was a significant negative relationship between them and elevated CO₂ had no effect on it (Fig. 5).

Discussion

1. Effect of growth under elevated CO₂ on the capacity of photosynthesis and dark respiration in two radish cultivars differing in the capacity of storage root

The effects of growth under elevated CO₂ on the photosynthetic capacities at different developmental stage were assessed using the first leaves of two cultivars, K and WC at various ages. The capacities of photosynthesis changed considerably during development. Under the hydroponic cultures the growth rates of K and WC were quite high (data not shown, for K see accompanying paper, Usuda 2004). The high growth rate including mutual shading seemed to be resulted in relatively fast senescence, which caused significant changes in the rate of photosynthesis during the experimental period. There was, however, essentially no effect of elevated CO₂ on the photosynthetic capacities. In K Pgmax and transpiration and the values of qP, Fv/Fm, ΦPSII and Fv'/Fm' decreased during development slightly faster under elevated CO₂ than under ambient CO₂ (Fig. 1). In this cultivar, the rate of dark respiration and the value of qN were not affected by elevated CO₂ (Fig. 1). In WC, Pgmax and the values of qP, and ΦPSII decreased during development slightly faster under elevated CO₂ than under ambient CO₂ (Fig. 2). In young WC the values of Fv/Fm and qN were increased by elevated CO₂. However, the effects of growth under elevated CO₂ on the rates of transpiration and dark respiration and the values of Fv'/Fm' were not observed. A slight change in the effect of elevated CO₂ depending on the developmental stage found in this study seemed
to be due to the acceleration of ontogeny by elevated CO2. Acceleration of ontogeny of a very young leaf had a slightly positive effect on the maximum intrinsic capacity of photosynthesis under elevated CO2 as discussed above. These results indicate that at least in the two cultivars of radish, exposure to elevated CO2 does not cause down regulation of the maximum capacity of photosynthesis, and that a slightly earlier decline in the capacity of photosynthesis under elevated CO2 is due to the acceleration of ontogeny. Kosena lacks a large storage root but the increase in total biomass caused by elevated CO2 was larger than that in WC (this study; Usuda et al., 1999a, b; Usuda and Rouheir, 2001). The growth rate of K grown under similar conditions to this study was quite high (the accompanying paper, Usuda, 2004), suggesting that vigorously developing leaves of K play an important role as a sink in utilizing increased carbohydrates in the leaves to clarify the effect of growth under elevated CO2 are needed.

The rate of dark respiration was high in young leaves and it decreased with aging. There was no effect of growth under elevated CO2 on the rate of dark respiration (Fig 1b, 2b). This is consistent with the recent finding of Jahnke and Krewitt (2002). For further discussion see accompanying paper (Usuda, 2004).

2. Changes in the rate of photosynthetic CO2 assimilation and chlorophyll fluorescence during development

As discussed above the effect of growth under elevated CO2 on the capacity of photosynthesis was rather small in the two cultivars of radish. The photosynthetic characters, however, changed substantially during development (Fig 1, 2). The analyses of the relationship between the capacity of CO2 fixation and chlorophyll fluorescence should give us general insight into changes in the photosynthetic characters during development or senescence. The maximum Pmax decreased with advancing age. There was a significant positive relationship between the initial slope of A-C curve and the Pmax (Fig. 3). One of the causes of the decline in the capacity of photosynthesis during development or senescence is the decline in the activity of ribulose 1,5-bisphosphate carboxylase in situ. To understand the changes in capacities other than carboxylation during development or senescence the relationships between ΦCO2 and ΦPSII, qP, F'/Fm' and qN were examined (Fig.4). The condition used to determine these parameters were 1,200 μmol photons m-2 s-1 and 1,000 μmol mol-1 CO2 in the inlet air containing 21% O2. This condition was referred to a low-photorespiratory condition. There was a linear relationship between ΦCO2 and ΦPSII. Previously many reports found a linear relationship between ΦCO2 and ΦPSII under non- or low-photorespiratory conditions with changing light intensity (Genty et al., 1989; Genty et al., 1990; Marco et al., 1990; Baker, 1991; Krall and Edwards, 1992; Edwards and Baker, 1993; Valentini et al., 1995; Habash et al., 1995). The slopes of the straight line under ambient and elevated CO2 were 8.66 and 8.81, respectively in K and 7.70 and 8.19, respectively in WC. These values were close to the theoretical minimum value of 8, if equal energy was absorbed by photosystem I and II and 4 electrons were required to fix one molecule of CO2. The rate of respiration in the light other than photorespiration was assumed to be the same as that of dark respiration in this study. If it caused an overestimation of the rate of respiration under light then the values of slope became larger. The overestimation seemed to be very small, however, because the rate of respiration was rather small compared with the rate of photosynthetic CO2 fixation. The values of intercept of the straight lines were close to zero. Actually the values under ambient versus elevated CO2 were 0.03 and 0.027, respectively in K and 0.081 and 0.054, respectively in WC. These small positive values indicated that the fractions of electron transport used for the process other than photosynthetic fixation of CO2 under the low-photorespiratory condition were very small. These relationships between ΦCO2 and ΦPSII were found in the leaves having different maximum photosynthetic capacities under constant light intensity of near saturation. These results indicate that the linear relationship was a very general character and chlorophyll fluorescence analysis can be used to evaluate the rate of CO2 assimilation under various conditions. The decrease in ΦPSII, namely the quantum yield of electron transport from photosystem II, were derived from both the decrease in qP, namely the photochemical quenching and the decreased F'/Fm', namely efficiency with which absorbed quanta are transferred to the open PSII reaction centers. One of the mechanisms of lower photochemical quenching in old leaves was the lower activity of ribulose 1,5-bisphosphate carboxylase in situ (Fig. 3). Other mechanisms responsible for lower photochemical quenching remain to be elucidated.
There were significant negative relationship between $\Phi CO_2$ and qN and also between $F'_v/F_m'$ and qN. It suggests that with aging the capacity of non-photochemical quenching increased and it resulted in lower efficiency with which absorbed quanta are transferred to the open PSII reaction centers. The values of $F'_v/F_m'$ stayed high during aging or senescence except in very old leaves indicating that the maximum intrinsic quantum yield of PSII was relatively stable during aging or senescence (Fig. 1g, 2g). All these results indicated that during aging or senescence when the rate of photosynthetic CO2 assimilation decreased, the capacity of carbon metabolism (represented by the activity of ribulose 1,5-bisphosphate carboxylase in situ) and the photochemical capacity (represented by $q_P$ and $F'_v/F_m'$) decreased coordinately. Growth under elevated CO2 has almost no effect on this process although growth under elevated CO2 had a small effect on the relationship between $\Phi CO_2$ and qN with K (Fig. 4c). Growth under elevated CO2 might have small negative effects on the capacity of non-photochemical quenching with relatively old leaves, the mechanisms of which are not clear.

**Conclusions**

Growth under elevated CO2 did not cause down regulation of the maximum capacity of photosynthesis suggesting that there was no down regulation of the expression of the photosynthetic gene transcripts by CO2 enrichment in the two cultivars of radish, one with a large storage root and the other growing vigorously without a large storage root. Not only the storage root, but also vigorously growing young leaves seemed to play an important role as a sink in utilizing increased photosynthate during growth under elevated CO2. Growth under elevated CO2 accelerated ontogeny, and caused a slightly earlier decline in the capacity of photosynthesis. During aging the rate of photosynthetic fixation of CO2 declined, and the capacity of carbon metabolism and photochemical capacity decreased coordinately.

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