Summary of Doctoral Thesis

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Title	Effects of elevated atmospheric carbon dioxide concentration on growth, photosynthesis and morphology in Chinese yam (大気中の高濃度二酸化炭素がナガイモの生長、光合成および形態に及ぼす影響に関する研究)

The increase in carbon dioxide (CO_2) is widely being considered as the main driving factor that caused the phenomenon of global warming. The effects of elevated atmospheric CO_2 concentration ([CO_2]) on growth of plants such as rice, wheat, soybean, potato etc have been studied but, to date, no experiments related to the effects of elevated [CO_2] have been performed in yam, including Chinese yam. To determine the effective strategies for yam cultivation under the future climatic change, it is important to understand how Chinese yam responds to elevated [CO_2] and by which mechanism the responses occur. This study was carried out with the purpose to elucidate the effects of elevated [CO_2] on growth, photosynthesis and morphology in Chinese yam.

Firstly, to understand the effects of elevated [CO_2] on growth, photosynthesis in Chinese yam, two experiments were conducted in temperature-gradient chambers. Summer experiment was carried out from 11 July to 3 September, 2015 and autumn experiment was carried out from 23 August to 3 October, 2015 with Chinese yam line Enshikei 6 in the chambers. [CO_2] and air temperature were controlled independently in each temperature-gradient chamber. Two temperature-gradient chambers were used under two [CO_2] conditions: ambient (averaged 400 μmol mol^{-1}) and elevated (ambient [CO_2] + 200 μmol mol^{-1} in daytime (0400 to 2030), averaged 600 μmol mol^{-1}). Each chamber was a naturally sunlit greenhouse. In each temperature-gradient chamber, two treatment plots were set along an air temperature-gradient: approximately ambient-temperature plot and high-temperature plot. Thus, in the experiments, Chinese yam was grown at ambient [CO_2] and elevated [CO_2] under approximately ambient- and high-temperature regimes in summer and autumn, separately. For comparison, rice was also grown under these conditions. Mean air temperatures in the approximately ambient- and high-temperature plots were respectively 24.1°C and 29.1°C in summer experiment and 20.2°C and 24.9°C in autumn experiment. In summer experiment, Chinese yam vine length, leaf area, leaf dry weight (DW), and total DW were significantly higher under elevated [CO_2] than ambient [CO_2] in both approximately ambient- and high-temperature regimes. Additionally, number of leaves, vine DW, and root DW were significantly higher under elevated [CO_2] than under ambient [CO_2] in the approximately ambient-temperature regime. In autumn experiment, tuber DW was significantly higher under elevated [CO_2] than under ambient [CO_2] in the high-temperature regime. These results demonstrate that yam shows positive growth responses to elevated [CO_2]. Elevated-to-ambient [CO_2] ratios of all growth parameters related to size and weight in summer experiment were higher in Chinese yam than in rice. Analysis of variance revealed that elevated [CO_2] more strongly affected most growth parameters except for total DW in Chinese yam than in rice in summer experiment. The results suggest that the contribution of elevated [CO_2] is higher in Chinese yam than that in rice under summer conditions. Net photosynthetic rate in Chinese yam was significantly higher under elevated [CO_2] than under ambient [CO_2] in both temperature regimes in summer experiment and showed an increasing trend from ambient [CO_2] to elevated

$[CO_2]$ in autumn experiment. However, in rice, no significant differences in net photosynthetic rate were detected between ambient $[CO_2]$ and elevated $[CO_2]$ in summer and autumn experiments. These findings indicate that photosynthesis responds more readily to elevated $[CO_2]$ in Chinese yam than in rice.

Secondly, to investigate the effects of elevated $[CO_2]$ on the germination of seed bulbils and the seedling vigour of Chinese yam, two Chinese yam lines, Enshikei 6 and Shojikei, were used in this experiment in the temperature-gradient Chambers. Seed bulbils were sown at 4 June, 2016 and seedlings germinated from seed bulbils were grown until 9 July, 2016 under two $[CO_2]$ levels, ambient (averaged 400 $\mu mol\ mol^{-1}$) and elevated (ambient + 200 $\mu mol\ mol^{-1}$ in day time (0400 to 2030), averaged 600 $\mu mol\ mol^{-1}$) and two mean air temperature conditions, 22.2°C and 25.6°C. The results showed that elevated $[CO_2]$ did not affect bulbil germination of either Chinese yam lines. During the early growth stage, the DWs of leaves, vines, shoots, roots, belowground parts (roots + tubers) and whole plants were higher under elevated $[CO_2]$ than under ambient $[CO_2]$ for both Chinese yam lines under the approximately ambient- and high-temperature regimes. The values of vigour indexes (index I = germination % × seedling length and index II = germination % × seedling DW) were also higher under elevated $[CO_2]$ than under ambient $[CO_2]$ for both lines. These results indicated that Chinese yam seedlings respond positively to elevated $[CO_2]$ during the early growth stage. The below:aboveground DW ratios were higher under elevated $[CO_2]$ than under ambient $[CO_2]$ in seedlings with very small new tubers for both yam lines, indicating that elevated $[CO_2]$ strongly affected the roots starting in the early growth stage. The DWs of post-treatment seed bulbils were higher with elevated $[CO_2]$ than ambient $[CO_2]$ under both temperature regimes. The results showed that Chinese yam seedling used a smaller amount of the reserves in seed bulbils under elevated $[CO_2]$ than under ambient $[CO_2]$ conditions. Therefore, the results show that elevated $[CO_2]$ is a positive resource for seedling growth in the Chinese yam lines.

Thirdly, to investigate the effects of elevated $[CO_2]$ on leaf morphology of these two Chinese yam lines under the same experiment conditions as described above in the "secondly" section, bright-field optical microscopy and transmission electron microscopy were used to observe the inner structure of leaf blade tissues and scanning electron microscopy was used to observe stomata density and size in yam leaf blade. The palisade layer was thicker under elevated $[CO_2]$ than under ambient $[CO_2]$ in both temperature regimes, and the whole yam leaf blade was thicker under elevated $[CO_2]$ than under ambient $[CO_2]$ in the approximately ambient temperature regime. The results indicated that elevated $[CO_2]$ increased the yam leaf blade thickness by increasing the cell size of palisade tissues. The numbers of chloroplasts per palisade cell and spongy cell, the number of starch grains per chloroplast, profile area of the starch grain, and starch-to-chloroplast area ratio in both palisade and spongy cells were higher under elevated $[CO_2]$ than under ambient $[CO_2]$ in both temperature regimes. Furthermore, the stomatal density on the abaxial side of the leaf blade in Chinese yam was greater under elevated $[CO_2]$ than under ambient $[CO_2]$ in both temperature regimes, and stomatal-pore length was higher under elevated $[CO_2]$ than under ambient $[CO_2]$ in the approximately ambient temperature regime. These results indicate that elevated $[CO_2]$ positively affects the photosynthetic apparatus and enhances photosynthesis. The results of this study provide important information and a possible explanation for the positive photosynthetic responses of Chinese yam to elevated $[CO_2]$ in our previous study.

To our knowledge, this is the first temperature gradient chamber study that investigated effects of elevated CO_2 concentration on growth and photosynthesis and morphology in Chinese yam. The study shows that elevated $[CO_2]$ increased the thickness of palisade layer and whole leaf blade, numbers of stomata, chloroplasts and starch grains in yam leaves. Consequently, elevated $[CO_2]$ enhanced the net photosynthetic rate. In addition, number of leaves and leaf blade

area also increased with elevated [CO_2]. Thus, the results leaded to increase in yam plant DW, including tuber DW, under elevated [CO_2] than under ambient [CO_2]. The knowledge on the effects of elevated [CO_2] on growth, photosynthesis and morphology in Chinese yam presented in this study will contribute for understanding the characterization of responses to elevated [CO_2] in yam and for yam production and breeding to make sustainable production in northern Japan under the climate change in the future.

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