Effects of Long-term Exposure to Different O₂ Concentrations on Growth and Phytochemical Content in Red Leaf Lettuce

Shun-Ichiro KAWASAKI1, JUN TOMINAGA1,2, NAOKO UEHARA1, MASAMI UENO1 and YOSHINOBU KAWAMITSU1

1 Faculty of Agriculture, University of the Ryukyus, Nishihara, Okinawa 903-0213, Japan
2 The United Graduate School of Agricultural Sciences, Kagoshima University, Kagoshima 890-0065, Japan

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Oxygen gas is one of the environmental factors closely related to photosynthesis and respiration. In this article, we investigated the effects of long-term exposure to different O₂ concentrations on growth and phytochemical contents in leaf lettuce. In order for provide exposure to low O₂ for longer periods, we developed a new growth chamber combined with N₂ gas generator. Plants were hydroponically cultured under 3, 10 or 21% O₂. The leaf area of the plants grown at 3% O₂ was significantly smaller than that for plants grown at 21% O₂; however, there was no significant difference in dry weight. Owing to this, the specific leaf area of plants grown at 3% O₂ was significantly lower than that for plants grown at 21% O₂. While the nitrogen content of plants grown at 3% O₂ was significantly lower than that for plants grown at 21% O₂, the anthocyanin content of plants grown at 3 and 10% O₂ was significantly higher than that for plants grown at 21% O₂. According to results, we discussed that reduced leaf expansion observed in plants grown at low O₂ was the result of the decreased nitrogen.

Keywords: anthocyanin, long-term exposure, low oxygen, nitrogen content, photorespiration

INTRODUCTION

Environmental control is an important factor in increasing plant production in closed-type plant factories and extraterrestrial facilities such as space stations. Recently, there have been many studies on the plant production in closed systems (Rajapakse et al., 2009; Kozai, 2012; He et al., 2013). However, we still need to understand the relationship between environmental conditions and plant growth, photosynthesis, and phytochemical products under controlled conditions.

Oxygen gas is an environmental factor that is closely related to photosynthesis, photorespiration and respiration. It is well known that short-term exposure to 1% O₂ increases photosynthetic CO₂ fixation and decreases photorespiration in C₃ plants (Forrester et al., 1966a; 1966b). In addition, the leaf, stem and root dry weights of soybean plants were all increased by long-term exposure to 5% O₂ (Quebedeaux and Hardy, 1975). On the other hand, it was also reported that plant production and net photosynthetic rate were reduced by long-term exposure to low O₂ conditions. For instance, long-term exposure to 5% O₂ reduced the seed yield in soybeans (Quebedeaux and Hardy, 1975), and exposure to 2.5% O₂ reduced leaf expansion in several C₃ (rice, sorghum, wheat and spinach) and C₄ plants (barnyard millet) (Fukuyama et al., 1974a; 1974b; 1975; Takeda et al., 1978). From the results of experiments using C₃ plants, it was suggested that the decrease in leaf expansion was not related to photorespiration because C₄ plants has C₄ carbon cycle that is major carbon-concentrating mechanisms to minimize the photorespiration (Taiz and Zeiger, 2010). However, the cause of the reduction in leaf expansion remains to be elucidated. Furthermore, it was shown that long-term exposure to low O₂ partial pressure (6 kPa) increased anthocyanin content in lettuce (Rajapakse et al., 2009; He et al., 2013). The mechanisms of the low O₂ concentration-related anthocyanin reactions also remain unclear.

The aim of our study was to investigate the long-term effects of O₂ concentration, as well as its interactions with other environmental factors, on plant growth, photosynthetic characteristics and phytochemical production in red leaf lettuce. In this article, we reported that effect of 20 days exposure to 3 or 10% O₂ concentration on plant growth, nitrogen, carbon, chlorophylls and anthocyanin contents in red leaf lettuce.

MATERIALS AND METHODS

Growth chamber design

Figure 1 shows the newly developed growth chamber used to determine the effects of long-term exposure to low O₂ in several plants. The chamber consists of two rooms; a low O₂ room in which the O₂ concentration can be controlled, and an ambient O₂ room in which the O₂ concentration is maintained at the ambient level. The size of each room is W 1,800 × D 1,000 × H 1,800 mm. The light source used in the experiments was a red and blue light-emitting diodes (RB-LEDs, Red:Blue=3:1, Civilight,
Taiwan). Temperature was controlled by an air conditioner (CS-F222CZW-W, Panasonic, Japan) and CO₂ level by the CO₂ controller (COC-1, Espec Mic, Japan). In order to control the O₂ level, N₂ gas was generated and introduced using an N₂ gas separation membrane system (NM-410A, Ube Ind., Japan). In the ambient room, air was pumped into the room at the same flow rate as for the low O₂ room. This growth chamber is an open system. The N₂ gas and air were introduced from the upper part of the chamber and removed from the bottom. The CO₂ concentration, temperature, relative humidity (RH), and O₂ concentration were continuously monitored by the CO₂ sensor (TR 9294, Air Test, Canada), thermocouple (Type T), RH sensor (HMP45D, Vaisala, Finland), and O₂ sensor (FCX-MVL-F, Fujikura, Japan), respectively. The signals from all the sensors were scanned every 10 s by the data logger (DA-100, Yokogawa, Japan).

**Plant materials and growth conditions**

Seeds of a variety of red leaf lettuce (*Lactuca sativa* L. var. crispa) were germinated in urethane cubes (2.0 × 2.0 × 2.5 cm) and grown in a plant growth cabinet for 14 days. In the growth cabinet, the temperature and photon flux density (PFD) were maintained at 21°C and 200 μmol m⁻² s⁻¹ using white fluorescent lamps, respectively, with a 12-h light/dark cycle. The plants were supplied with water for the first 7 days from germination, followed by liquid fertilizer (Hyponica, KYOWA, Japan). The plants were then transplanted to another growth cabinet and grown with liquid fertilizer for 7 days prior to low O₂ treatment. The temperature and PFD in the growth cabinet were maintained at 21°C and 200 μmol m⁻² s⁻¹ (LEDs, Red:Blue = 3:1, Civilight, Taiwan), respectively.

**Effect of long-term exposure to 3 and 10% O₂ concentrations**

**Experiment 1: Long-term exposure to 3% O₂ concentration**

Long-term exposure to 3% O₂ was undertaken for 20 days using 24 red leaf lettuce plants per room. The O₂ concentration in the low O₂ room was set at 3% O₂ during light period. Since the O₂ concentration was not controlled during the dark period, it rose to 17% O₂ or more. In the ambient O₂ room, the O₂ was maintained at 21% O₂. The flow rate of N₂ gas and air were set at 30 L min⁻¹. The total pressure was measured using a thermo recorder (RS-12P, Espec Mic, Japan). During low O₂ treatment, the total pressure in the low O₂ room was approximately 95.5 kPa, and this level was comparable to the almost total pressure (95.3 kPa). The CO₂ concentration was kept at 400 μmol mol⁻¹ during the light period. The temperature and PFD (RB-LEDs light source) in the chamber were maintained at 21°C and 250 μmol m⁻² s⁻¹, respectively. The RH was kept at 80±5% during the light period and 95±5% during the dark period. The plants were grown with liquid fertilizer (pH 6.3 and EC 1.27 mS cm⁻¹) containing 450 mg L⁻¹ NO₃-N, 10.1 mg L⁻¹ NH₄-N, 40.9 mg L⁻¹ P, 169.4 mg L⁻¹ K, 68.3 mg L⁻¹ Ca, 18.6 mg L⁻¹ Mg, 0.52 mg L⁻¹ Mn, 0.41 mg L⁻¹ B, and 1.54 mg L⁻¹ Fe. Aeration was conducted in the liquid fertilizer tank, and the air was introduced from outside of the chamber. Dissolved oxygen was measured by optical oxygen meter (Fibox 3, PreSens, Germany) after low O₂ treatment, and that in liquid fertilizer was approximately 19.3% O₂ at each treatment. The light source, CO₂

![Fig. 1](image1.png)

**Fig. 1** A schematic view of the newly developed growth chamber. The double lines represent the gas flow line, and the black line from each sensor represents the cable.

![Fig. 2](image2.png)

**Fig. 2** Red leaf lettuce grown for 20 days at 3, 10 or 21% of O₂ concentrations under 400 μmol mol⁻¹ CO₂.
controller, and hydroponic system pumps were switched on at the start of each light period and off at the start of each dark period. The N\textsubscript{2} gas generator was switched on at 3-h before the start of each light period as 3-h were required to reach low O\textsubscript{2} condition. After exposure to low O\textsubscript{2} concentration for 20 days, 6 plants in each treatment was harvested to check leaf number, fresh weight, leaf and root dry weight (after drying for 72 h at 80°C), and leaf area (LI-3100, Li-Cor, USA). After drying, samples were powdered and used for analysis of leaf nitrogen and carbon, and minerals analysis.

**Experiment 2: Long-term exposure to 10% O\textsubscript{2} concentration**

Long-term exposure to 10% O\textsubscript{2} was undertaken for 20 days using 24 red leaf lettuce plants per room. The O\textsubscript{2} concentration in the low O\textsubscript{2} room was set at 10% O\textsubscript{2} during light period. Since the O\textsubscript{2} concentration was not controlled during the dark period, it rose to 17% O\textsubscript{2}, or more. In the ambient O\textsubscript{2} room, the O\textsubscript{2} was maintained at 21% O\textsubscript{2}. Room temperature, relative humidity, CO\textsubscript{2} concentration and liquid fertilizer conditions, machine ON/OFF time and analysis items were same as experiment 1.

**Total nitrogen, total carbon and mineral analysis**

The 25 mg dry powder samples were prepared for the analysis. Leaf nitrogen and carbon contents were analyzed by N/C analyzer (NC-90A, Shimadzu, Japan).

Leaf minerals were analyzed by plasma-emission-spectrometry (ICPS-8100, Shimadzu, Japan). The 250 mg dry powder samples were extracted with 50 ml of 0.5% HNO\textsubscript{3} overnight in a water bath at 80°C. The samples were filtered using No. 6 filter paper (Advantec, Japan) prior to analysis.

**Chlorophylls and anthocyanin analysis**

For analysis of the chlorophyll content, 3 discs (2.4 cm\textsuperscript{2}) per plant were punched from the fully expanded leaf. The discs were extracted with 2 ml of 99.7% methanol overnight in dark at 12°C. The spectrum readings were recorded at 665.2 and 652.0 nm using a spectrophotometer (UV-1600PC, Shimadzu, Japan) (Porra et al., 1989).

For analysis of the anthocyanin, 5 plants were harvested and immediately freeze-dried for 72-h. Thereafter, the dry samples were powdered and 100 mg powdered sample was extracted with the 10 ml of 99.7% methanol: 1.5 N HCl (85: 15, v/v) overnight in dark at 12°C. Spectra were recorded at 533.0 nm and calculated as cyanidin-3-gulcoside (Iwai et al., 2009).

**Statistical analysis**

Six samples were used for statistical analysis in growth parameters, nitrogen, carbon, chlorophylls and minerals content (n = 6). Five samples were used for statistical analysis in anthocyanin content (n = 5). Differences among the mean values for each treatment were analyzed using Mann-Whitney U test (MWU test) with a P value < 0.01 and 0.05 considered to be statistically significant.

**RESULTS**

**Experiment 1: Long-term exposure to 3% O\textsubscript{2} concentration**

Plants grown at 3% O\textsubscript{2} concentration had more red pigmentation than those grown at 21% O\textsubscript{2}, and plants grown at 3% O\textsubscript{2} was smaller than plants grown at 10 and 21% O\textsubscript{2} (Fig. 2). There were no significant differences in leaf number between 3 and 21% O\textsubscript{2} (Table 1). The leaf area of plants grown at 3% O\textsubscript{2} was significantly smaller than that for plants grown at 21% O\textsubscript{2}. There was no significant difference in leaf fresh and dry weight, and root dry weight between 3 and 21% O\textsubscript{2}. From leaf area and leaf dry weight results, the specific leaf area (SLA) of plants grown at 3% O\textsubscript{2} was found to be significantly lower than that of plants grown at 21% O\textsubscript{2}. The SLA represents a given biomass spread over a small or large leaf area (Evans and Poorter, 2001). The results showed that the leaves of plants grown at 3% O\textsubscript{2} were thicker than those grown at 21% O\textsubscript{2}.

The leaf nitrogen content of plants grown at 3% O\textsubscript{2} was significantly lower than that for plants grown at 21% O\textsubscript{2} (Fig. 3). On the other hand, there was no significant difference in carbon content between 3 and 21% O\textsubscript{2}. Chlorophylls analysis revealed that chlorophyll b content of plants grown at 3% O\textsubscript{2} was significantly higher than that for plants grown at 21% O\textsubscript{2} (Fig. 4). However, there were no significant differences in chlorophyll a or a + b contents between 3 and 21% O\textsubscript{2}. Consistent with visual observations, the anthocyanin content of plants grown at 3% O\textsubscript{2} was significantly higher than that for plants grown at 21% O\textsubscript{2} (Fig. 5). The phosphate level of plants grown at 3% O\textsubscript{2} was significantly higher than those for plants grown at 21% O\textsubscript{2}, while plants grown at 3% O\textsubscript{2} had the lowest potassium and sulfate levels (Table 2).

**Experiment 2: Long-term exposure to 10% O\textsubscript{2} concentration**

The results of leaf number, leaf area, leaf fresh and dry weight, and root dry weight were same as experiment 1 (Table 1). However, there was no significant difference between 21% O\textsubscript{2} in SLA. In leaf nitrogen, carbon and chlorophylls contents, there were no significant difference between 10 and 21% O\textsubscript{2} (Figs. 3 and 4). On the other hand, anthocyanin content of plants grown at 10% O\textsubscript{2} was significantly higher than that for plants grown at 21% O\textsubscript{2} (Fig. 5). In mineral analysis, there were no significant difference in

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**Table 1**  
Plants growth of red leaf lettuce grown for 20 days at 3, 10 or 21% O\textsubscript{2} concentrations under 400 μmol mol\textsuperscript{−1} CO\textsubscript{2}.

| O\textsubscript{2} conc. (%) | No. of leaves (No./plant) | Leaf area (cm\textsuperscript{2}/plant) | Leaf FW (g/plant) | Leaf DW (g/plant) | Root DW (g/plant) | SLA (cm\textsuperscript{2} mg\textsuperscript{−1}) |
|-----------------------------|---------------------------|-----------------------------------------|------------------|-----------------|------------------|------------------------------------------|
| 3                           | 13.5                      | 503.3                                   | 27.8             | 1.44            | 0.23             | 0.35                                     |
| 21                          | 14.7                      | 700.8*                                  | 31.3             | 1.34            | 0.24             | 0.53**                                   |
| 10                          | 13.8                      | 767.5*                                  | 33.0             | 1.72            | 0.23             | 0.45                                     |
| 21                          | 14.5                      | 963.9*                                  | 38.5             | 2.00            | 0.27             | 0.49                                     |

Note: ** and * indicate the significant difference at P < 0.01 and 0.05 by MWU test, respectively (n = 6).
any mineral components between 10 and 21% O₂ (Table 2).

DISCUSSION

The N₂ gas generator system that was combined with the new growth chamber has often been used in experiments related to storage systems for fruits and vegetables (Kawagoe et al., 1991; Dan et al., 1994; Chapon et al., 2004). In this experiment, we successfully grew leaf lettuce under low O₂ concentrations for two weeks using this N₂ gas generator system. Generally, a large number of N₂ gas cylinders are needed to maintain low O₂ concentrations for an extended period. However, the use of this N₂ gas generator abolished the need for N₂ gas cylinders.

In the present experiment, the SLA of plants grown at 3% O₂ was significantly lower than that of plants grown at 21% O₂ (Table 1). Fukuyama et al. (1974a; 1974b, 1975) and Takeda et al. (1978) reported decreased leaf expansion for several C₃ and C₄ plants grown under 2.5% O₂. Iwabuchi et al. (1996) and Rajapakse et al. (2009) also reported the thickening of leaves in leaf lettuce grown under low O₂ partial pressures (6 and 10 kPa). It is also known that plant cell walls become thicker with reduced nitrogen absorption (Larcher, 2003). In the present experiment, the nitrogen content of the plants grown at 3% O₂ was significantly lower than that of plants grown at 21% O₂ (Fig. 3). Rajapakse et al. (2009) also reported a reduction in nitrogen content under low O₂ partial pressure. Therefore, it was speculated that the reduction in nitrogen content ascribed to the leaf thickening.

In general, nitrogen absorption requires energy for ion absorptions, and the energy for nitrogen absorption is dependent on dark respiration (Larcher, 2003). It is known that respiration rates decrease if the atmospheric O₂ is below 5% for whole organs or below 2 and 3% for tissue slices (Taiz and Zeiger, 2010). Therefore, it was thought that dark respiration would not be affected by O₂ as the concentration returned to over 17% during the dark period. Takeda et al. (1978) found reductions in leaf expansion in C₃ and C₄ plant types. Moreover, they pointed out that the reduction was induced only during the light period. From these results, it was speculated that the leaf expansion response was not related to dark respiration or photorespiration, but occurred as a reaction to light. The actual light reaction affected by low O₂ concentrations remains still unclear. Iwabuchi et al. (1996) showed that the dry weight of spinach was not affected by low O₂, whereas the fresh weight and leaf expansion was reduced. They were uncertainty as to the reason for these conflicting
results, and suggested that the effect of low O2 on plant growth species dependent in that while dry weight was generally enhanced by low O2 conditions (Fukuyama et al., 1974a; Quebedeaux and Hardy, 1975), this was not true for all plants species (Priestley et al., 1988; Iwabuchi et al., 1996). Priestley et al. (1988) also reported a reduction in leaf expansion, and showed that low O2 reduced respiratory losses from leaves as well as reducing the proportion of soluble carbohydrate converted to polysaccharide. In the present experiment, although there were no significant differences in the leaf carbon content per unit dry weight among the O2 concentrations (Fig. 3), carbon content per unit leaf area of plants grown at 3% O2 was significantly higher than those for plants grown at 10 and 21% O2 (data not shown). Therefore, the increase in leaf thickness observed under low O2 concentrations could be due to an increase in carbohydrate content in the leaves.

Rajapakse et al. (2009) reported decreases of potassium and sulfite contents at low O2 partial pressure, however, there was no significant difference in phosphate content. They argued that the reduction in leaf mineral content could be attributed to poor root growth, which inhibited mineral uptake (He et al., 2007; Rajapakse et al., 2009). In their experiment, calcined clay was used to grow plants, whereas hydroponics was used in the present experiment. Root growth increased at hydroponic conditions as compared to soil, therefore there was no significant differences in root dry weight of plants grown at low O2 concentrations. However, from results of potassium and sulfite levels, it is possible that mineral uptake was inhibited at 3% O2 concentration.

The anthocyanin content of plants grown at 3 and 10% O2 was significantly higher than that of plants grown at 21% O2. Rajapakse et al. (2009) and He et al. (2013) also reported an increase in anthocyanin content in plants grown under low O2 partial pressure. While Rajapakse et al. (2009) suggested that ethylene was one of the factors contributing to increased leaf anthocyanin content, they noted that ethylene was not the sole cause of the increased anthocyanin production under hypoxia (low O2 conditions). Under low O2 conditions, photosynthesis is inhibited; however, the role of photorespiration remains unclear. It is assumed that photorespiration is one means of effectively dissipating excess photochemical energy (Powles and Osmond, 1979). Kozaki and Takeba (1996) demonstrated that photorespiration drives electron transport and protects plants from photooxidation. From this, the plants grown at low O2 were suspected of being susceptible to light stress.

In the other low O2 treatment studies, metal halide lamp was used as a light source (Rajapakse et al., 2009; He et al., 2013), whereas RB-LEDs was used in the present experiment and the PFD was 250 μmol m–2 s–1. The intensity of RB-LEDs is below the level at which photoinhibition occurs. However, one of the characteristics of LEDs is that it can produce specific wavelengths; i.e., the plants were exposed to red (660 nm) and blue (450 nm) wavelengths in the present experiment. Shoji et al. (2010) evaluated the relationship between wave length and anthocyanin content in leaf lettuce and showed that blue LEDs increased anthocyanin content. In present experiment, we did not measure the effects of blue-LEDs on anthocyanin produce, however there is a possibility that blue-LEDs condition affected the increase in anthocyanin content. Future studies are needed to evaluate the relationship between O2 concentration and light conditions in greater detail. Moreover, anthocyanin is currently gaining attention as a functional ingredient in Japan (Igarashi, 2004). In the future, O2 concentration control may be used in new cultivation system in order to increase anthocyanin content.

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REFERENCES

Chapon, J. F., Blanc, C., Varoquaux, P. 2004. A modified atmosphere system using a nitrogen generator. Postharvest Biol. Technol. 31: 21–28.

Dan, K., Higashiyama, M., Nagata, M., Yamashita, I. 1994. Development of gas separation membrane-modified air system / CO2 evolution analyzer for determining respiration of fruits and vegetables under low oxygen atmosphere: Studies on sensitivity of vegetables to low oxygen Part 1. (in Japanese with English summary) J. Jpn. Soc. Cold Preserva. Food 20: 143–146.

Evans, J. R., Poorter, H. 2001. Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. Plant Cell Environ. 24: 755–767.

Forrester, M. L., Krotkov, G., Nelson, C. D. 1966a. Effect of oxygen on photosynthesis, photorespiration and respiration in detached leaves. I. Soybean. Plant Physiol. 41: 422–427.
Forrester, M. L., Krotkov, G., Nelson, C. D. 1966b. Effect of oxygen on photosynthesis, photorespiration and respiration in detached leaves. II. Corn and other monocotyledons. Plant Physiol. 41: 428–531.

Fukuyama, M., Takeda, T., Taniyama, T. 1974a. Studies on the effects of oxygen concentration on the photosynthesis and the growth of crop plants. I. The effects of oxygen concentration under various growth temperatures on the growth of wheat and rice plants. (in Japanese with English summary) Proc. Crop Sci. Soc. Jpn. 43: 267–277.

Fukuyama, M., Takeda, T., Maeda, H. 1974b. Studies on the effects of oxygen concentration on the photosynthesis and the growth of crop plants. II. Relationship between photorespiration and expansion of leaf area. (in Japanese with English summary) Proc. Crop Sci. Soc. Jpn. 43: 453–461.

Fukuyama, M., Takeda, T., Oshiro, S. 1975. Studies on the effects of oxygen concentration on the photosynthesis and the growth of crop plants. III. Effect of low oxygen concentration treatment for comparatively long period on the growth in two row barley. (in Japanese with English summary) Proc. Crop Sci. Soc. Jpn. 44: 1–6.

He, C., Davies Jr, F. T., Lacey, R. E. 2007. Separating the effects of hypobaria and hypoxia on lettuce: growth and gas exchange. Physiol. Plant. 131: 226–240.

Igarashi, K. 2004. A variety and functions of anthocyanins in foodstuffs: centering around atsumi-kabu. (in Japanese) J. Integr. Stud. Diet. Habits 15: 4–11.

Iwabuchi, K., Goto, E., Takakura, T. 1996. Germination and growth of spinach under hypobaric conditions. Environ. Control Biol. 34: 169–178.

Iwai, M., Ohta, M., Tsuchiya, H., Suzuki, T. 2009. Effect of simultaneous light irradiation with blue-LEDs and fluorescent lamps for improving anthocyanin production in young leaves of red perilla (Perilla frutescens L.). (in Japanese with English summary) J. SHITA 21: 51–58.

Kawagoe, Y., Morishima, H., Seo, Y., Imou, K. 1991. Development of CA-Storage system with gas separation membrane (Part 1): Apparatus and its performance. J. JSAM 53: 87–94.

Kozai, T. 2012. Plant factory with artificial light. (in Japanese) Ohmsha, Tokyo, pp 166.

Kozai, T., Takeba, G. 1996. Photorespiration protects C3 plants from photooxidation. Nature 384: 557–560.

Larcher, W. 2003. Physiological plant ecology, Ed. 4, Springer-Verlag, Berlin, pp 203.

Porra, R. J., Thompson, W. A., Kriedemann, P. E. 1989. Determination of accurate extinction coefficients and simultaneous equations for assaying chlorophylls a and b extracted with four different solvents: verification of the concentration of chlorophyll standards by atomic absorption spectroscopy. Biochim. Biophys. Acta 975: 384–394.

Powles, S. B., Osmond, C. B. 1979. Photoinhibition of intact attached leaves of C3 plants illuminated in the absence of both carbon dioxide and of photorespiration. Plant Physiol. 64: 982–988.

Priestley, C. A., Treharne, K. J., Lenz, F. 1988. Effects of low oxygen on photosynthesis, translocation and growth in green pepper (Capsicum annuum). Ann. Bot. 61: 159–167.

Rajapakse, N. C., He, C., Cisneros-Zevallos, L., Davies Jr. F. T. 2009. Hypobaria and hypoxia affects growth and physicochemical contents of lettuce. Sci. Hortic. 122: 171–178.

Shoji, K., Goto, E., Hashida, S., Goto, F., Yoshihara, T. 2010. Effect of red light and blue light on the anthocyanin accumulation and expression of anthocyanin biosynthesis genes in red-leaf lettuce. J. SHITA 22: 107–113.

Taiz, L., Zeiger, E. 2010. Plant Physiology, Ed. 5, Sinauer Associates, Massachusetts, pp 330.

Takeda, T., Tsuchiya, M., Agata, W. 1978. Studies on the effects of oxygen concentration on the photosynthesis and the growth of crop plants. IV. The effect of subambient oxygen concentration during light or darkness on the growth and the leaf expansion of rice plant and barnyard millet. (in Japanese with English summary) Jpn. J. Crop Sci. 47: 344–353.