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Rate of Root Respiration of Lettuce under Various Dissolved Oxygen Concentrations in Hydroponics

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Knowledge on relationship between the rate of root respiration and dissolved oxygen (DO) concentration is essential for understanding the oxygen balance around roots in hydroponics. An airtight hydroponic system for the measurement of root respiration of lettuce was constructed. The initial concentrations of DO were 26 μmol·liter^{-1} ("treatment one-tenth"), 130 μmol·liter^{-1} ("treatment one-half"), 260 μmol·liter^{-1} ("treatment saturation"), and 380 μmol·liter^{-1} ("treatment over-saturation"). From the patterns of decreasing DO concentration during a 48 hr measurement period, the minimum DO concentration for root respiration and the rate of root respiration were calculated. The minimum DO concentration for the root respiration of lettuce 26 days after transplanting was around 78.2 μmol·liter^{-1}. The changes of DO concentration in treatments with plants four and ten days after transplanting were small.

The rate of root respiration was presented as a function of DO concentration, and increased as the DO concentration of nutrient solution increased. For DO concentrations in the range from 190 to 230 μmol·liter^{-1} which is usually observed in well aerated hydroponic beds, the rate of root respiration of lettuce 26 days after transplanting ranged from 2.9 to 6.7 μmol·hr^{-1}·(ml roots)$^{-1}$ at 23°C. In "treatment saturation," and larger root growth and greater amount of transpiration were attained in this treatment than in other treatments.

INTRODUCTION

Root zone aeration is essential to plants since it provides roots with the requisite oxygen for root respiration.[1,2] However, in hydroponics, gaseous oxygen barely reaches the root system. The roots can use only the oxygen dissolved in nutrient solution, and the saturation concentration of dissolved oxygen (DO) is very low (263 μmol·liter^{-1} at 23°C[3]). Jackson[4] and Morimoto *et al.*[5] reported that deep flow technique (DFT) systems can sometimes present serious problems of inadequate aeration to the roots, since the immersion of roots in unagitated water drastically reduces the diffusion of gases to the roots.

Attempts to achieve maximum root aeration have led to the development of various types of hydroponic culture systems for plant production. Nutrient film technique (NFT) was designed to maintain adequate root aeration by growing plants in a thin film of nutrient solution.[6] In principle, aeration of the roots in NFT should be at least as effective as in well drained soils.[7] However, it has been shown that deficient oxygen concentrations occur even in NFT systems.[8,9]

We paid attention to the roles of root system on deceasing DO concentration in hydroponics. The root system can affect nutrient fluid flow. The root mass

growing in a lump or root-mats in the small planting plates prevents the flow of nutrient solution through the roots. Root-lumping occurs especially in NFT that has only a small space for roots to spread out in the nutrient solution. In these circumstances, the mass flow of oxygen dissolved in nutrient solution is obstructed, and the roots that are not directly in the nutrient flow are likely to suffer from oxygen deficiency. However, there have been few studies on the characteristics of the flow of the nutrient solution in hydroponics and on the relationship between the flow characteristics and DO concentration.

Root systems can also change the local concentration of DO by root respiration. The rate of root respiration is dependent on the oxygen concentration around the roots, and the oxygen concentration is then determined by the amount of oxygen consumed by root respiration. Compared with numerous reports on the respiration of shoots and those of whole plants under various conditions, there have been few reports on root respiration itself. There have been some reports on root respiration but most of them are in the *in vitro* conditions.[10,11]

Therefore, knowledge of the rate of root respiration under certain DO concentrations is essential for understanding the oxygen balance around roots in hydroponic beds. In the present paper, root respiration rate of lettuce was measured under various DO concentrations to determine the amount of oxygen consumed by root respiration in areas of different local oxygen concentrations in the hydroponic beds. The effects of DO concentrations on root growth and transpiration were also studied. These data would be applied to a series of future studies on flow characteristics and DO concentrations in hydroponics.

MATERIALS AND METHODS

The experiment was carried out in an environmentally controlled room (23°C, 75% RH, 350 μmol·m^{-2}·sec^{-1} PPFD with fluorescent lamps). Leaf lettuces were prepared in DFT beds and were transplanted to a measuring box for measurement of root respiration. A regression model between root volume and days after transplanting was constructed to estimate the increase in root volume during the measurement period. A gas mixing box and a measuring box were constructed. Desired initial DO concentrations of nutrient solution in the measuring box were obtained by vigorously agitating the solution and adjusting the oxygen concentration in the gas mixing box. During the measurements, all valves around the measuring box were closed. The patterns of decreasing DO concentration of nutrient solution during the measurement period was monitored and represented by a regression equation. The rate of root respiration was derived from this equation, and was expressed as a function of DO concentration. Root growth and amount of transpiration during the measurement period were also studied.

Plant materials: Leaf lettuce (*Lactuca sativa* L. cv. Green wave) seeds were sown on polyurethane sponge and germinated in four day intervals. Roots of four day old seedlings were placed through holes (1 cm in diameter) in silicone stoppers, and were cultured in the hydroponic trays for four days as an initial adaptation period. Half-concentration of Yamazaki's nutrient solution was applied in this period. Table 1 lists the composition of the Yamazaki's solution. After the adaptation period, eight day old seedlings that developed uniform and well-formed root systems were selected and transplanted into the DFT beds. The seedlings had two leaves and their average seminal root length was 6.1 cm. Yamazaki's full concen-

Table 1 Composition of the nutrient elements of Yamazaki's solution used in this experiment.

Chemical name		Concentration
Macronutrients:	Potassium nitrate	4 meq·liter^{-1}
	Calcium nitrate	2 meq·liter^{-1}
	Monoammonium phosphate	1.5 meq·liter^{-1}
	Magnesium sulfate	1 meq·liter^{-1}
Micronutrients:	Copper (II) sulfate	0.02 mg·liter^{-1}
	Manganese sulfate	0.05 mg·liter^{-1}
	Zinc sulfate	0.05 mg·liter^{-1}
	Boric acid	0.50 mg·liter^{-1}
	EDTA-ferric salt	16.00 mg·liter^{-1}

tration nutrient solution was circulated continuously through the DFT beds and was changed every week to prevent low DO concentration. During the experiment, pH, electrical conductivity (EC) and DO concentration in the DFT beds were monitored and their values were kept stable.

Root growth measurement: It is necessary to know the volume of root system for determining the rate of root respiration. However, because the destructive method was adapted to determine the root volume, the root volume of plant at the beginning of measurement of root respiration could not be measured. Therefore, the initial root volume of plants used in measurement was estimated. Root volumes of the 236 plants from zero to 35 days after transplanting into the DFT beds were measured. A regression equation between the root volume and the number of days after transplanting was obtained. Average root volume at a certain date after transplanting was estimated from Eq. (1),

$$V=0.0698\times 1.1230^{d} \qquad (1)$$

where V is estimated volume of roots in ml, and d represents the number of days after transplanting. The R-squared value of regression analysis was 0.95.

Because the roots continue to grow during the measurement, it was also necessary to estimate the root growth during the 48-hr measurement. It was assumed that the root volume increased linearly during this period, because the interval of 48 hr was much shorter than the 36-day interval that root volumes were estimated from Eq. (1). The estimated initial root volume and the final root volume which were measured at the end of measurement, were used for the estimation of root volume linearly increased during the 48-hr measurement. The estimated root volumes were used in the calculation of root respiration rates.

For determination of root volume, a 10 ml measuring cylinder was used. The roots were removed from the shoots and dried for 15 min under natural shade before the measurements.

Root respiration measurement: In the present experiment, a DO sensor was used for the measurement of root respiration. Root respiration has been measured most commonly by the amount of carbon dioxide released,[12] and this amount has been converted to oxygen uptake by assuming a respiratory quotient (RQ) of 1.[10] Some reports, however, have pointed out that RQ should be different if the oxygen concentration changes.[11,13] Furthermore, in the anoxia conditions, anaerobic fermentation occurs, and this process does not use oxygen nor produce carbon dioxide.

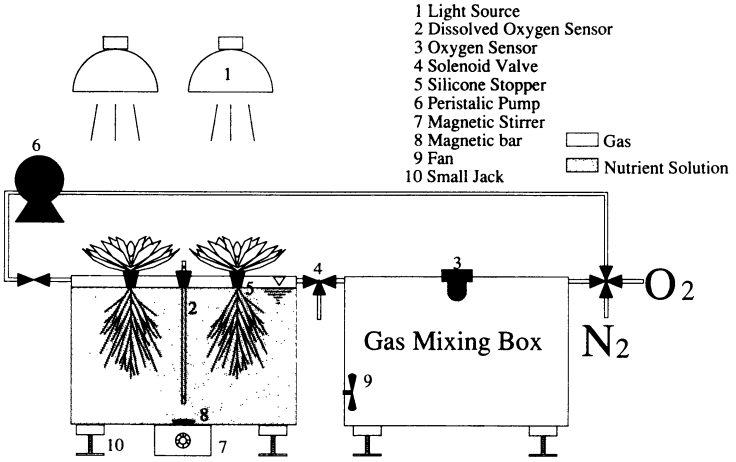

Fig. 1 A schematic diagram of an airtight hydroponic system for the measurement of root respiration under various DO concentrations.

Sensing the change in DO directly with a DO analyzer is a valid method to study the root respiration of hydroponically cultured plants because it is possible to eliminate the errors due to the RQ changes and anaerobic fermentation.

A schematic diagram of an airtight hydroponic system for the measurement of root respiration under various DO concentrations is shown in Fig. 1. Two airtight acrylic plastic boxes (L 30×W 30×H 19 cm) were constructed for the measurement of root respiration and for the gas mixing. A DO sensor (Model DCO-2, Toko Chemical Co., Tokyo) was located at a height of 5 cm from the bottom of the nutrient solution in the measuring box. The nutrient solution was stirred slowly (at about 250 rpm) with a magnetic stirrer and a 3 cm long magnetic bar.

Oxygen and nitrogen gases were supplied to the gas mixing box through the solenoid valves. A small fan was installed in the gas mixing box to mix the two gases uniformly. The measuring box was filled with 15.3 liter of Yamazaki's nutrient solution. The air in the 1.8 liter air space above the nutrient solution was circulated to the gas mixing box with a peristaltic pump (Model NE-5, Furue Sci., Tokyo). The nutrient solution in the measuring box was vigorously agitated by using a hand mixer (Model HM-250, Iuchi Co., Osaka). The oxygen concentration in the gas mixing box was monitored and controlled to maintain the desired DO concentration in the nutrient solution.

Vigorous agitation of the nutrient solution and high concentrations of oxygen and nitrogen gases were needed to reach the desired DO concentration. The agitation and high concentrations of gases were thought to be harmful to the roots, so the plants were placed in the measuring box only after the desired DO concentration was reached. After the desired DO concentration reached and maintained, all valves around the measuring box were closed, and four plants prepared in the DFT beds and mounted in silicone stoppers were set in the measuring box. It took two sec or less to set each plant into the measuring box, and it was confirmed from preliminary tests that the change of DO concentration during these several seconds was not significant. Thin silicone sheets were placed around the stems to prevent

gas leakage from the aerial part of the measuring box through pores in the urethane sponge. In the measuring box, there was gas space above the nutrient solution, but all roots were soaked in the solution. Plants at growth stages of 4, 10, and 26 days after transplanting to the DFT beds were used for measurements under four DO concentrations. Four initial DO concentrations were prepared, that is, 26 μmol·liter^{-1} (which is called "treatment one-tenth"), 130 μmol·liter^{-1} ("treatment one-half"), 260 μmol·liter^{-1} ("treatment saturation"), and 380 μmol·liter^{-1} ("treatment over-saturation").

By culturing four plants for 48 hr in the measuring box, the DO concentration data of the nutrient solution were collected by a microcomputer system. Oxygen concentrations of the gaseous portion were not measured, because it was calculated that the amount of oxygen diffused into the nutrient solution during the 48-hr measurement period is too small to affect the oxygen concentration of the gaseous portion. It was due to the low oxygen diffusivities in water (0.267 m^{-2}·sec^{-1} at 23°C).[3] All sets of the experiment were repeated three times.

Root respiration and DO concentration: A pattern of decreasing DO concentration with time was obtained when DO concentrations were plotted against time. Curve fitting by regression analysis was adapted, and the R^2 value was calculated for each case. The regression equation can be written as,

$$\exp(C)=\beta_0 t^{\beta_1}, \tag{2}$$

where C is concentration of DO in μmol·liter^{-1}, t is time of observation in hours, β_0 and β_1 are parameters of the model to be estimated. The unit of β_1 is μmol·liter^{-1}·hr^{-1}. In Eq. (2), as the time t approaches zero, the concentration C becomes infinite. Thus the data after five min were used in the regression analysis.

By using logarithmic transformation, Eq. (2) can be reduced to a linear regression model,

$$C=\beta_0^*+\beta_1 \ln t; \qquad t>0 \tag{3}$$

where β_0^* equals $\ln \beta_0$.

The R^2 value of the regression between C and $\ln t$ shows the degree of fitness between the estimated value of the DO concentration and the observed DO concentration. The rate of root respiration was derived from the derivative of Eq. (3) with respect to t. The rate of root respiration at a certain time is equal to the slope of the DO concentration at that time, as shown in Eq. (4),

$$\frac{V_{root}}{V_{soln}}R=\frac{dC}{dt}=\beta_1\frac{1}{t}; \qquad t>0 \tag{4}$$

where R is the rate of root respiration in μmol·hr^{-1}·(ml roots)$^{-1}$, and V_{soln} and V_{root} are volumes of solution in liter and roots in liter, respectively.

To know the relationship between the rate of respiration calculated from Eq. (4) and DO concentration around root system, another regression analysis was adapted,

$$R=\beta_2 e^{\beta_3 C}, \tag{5}$$

where β_2 and β_3 are parameters of the model to be estimated.

The t-test was applied to test the statistical significance of the regression models.[14]

RESULTS AND DISCUSSION

Changes of DO concentration

The time course changes in DO concentration of the nutrient solution in "treatment saturation," resulting from the effect of the different growth stages, are shown in Fig. 2. A rapid decrease in DO concentration was observed for plants at the growth stage of 26 days after transplanting. Compared to the treatments using plants of 26 days after transplanting, the changes of DO concentration in treatments with plants of four and ten days after transplanting were small. This suggests that the volume of nutrient solution was large and the volume of roots for the plants four and ten days after transplanting could not affect it. Therefore, these treatments were excluded from the analysis of rate of root respiration in the present experiment. However, this shows that to supply an ample amount of nutrient solution would be one method to overcome the DO deficiency problem.

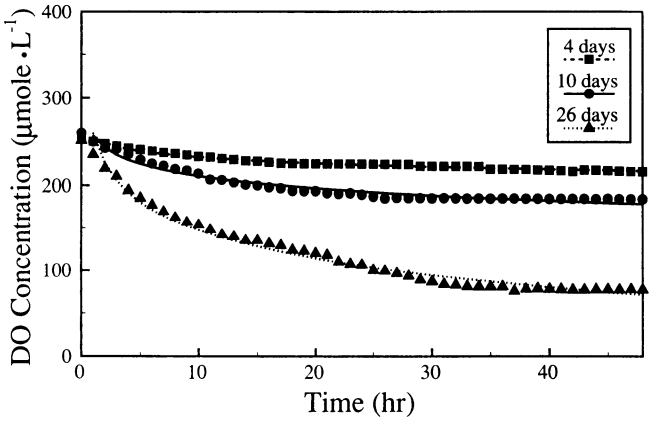

Fig. 2 Time course of DO concentration resulting from the effect of the four plants at the different growth stages. The initial DO concentration was saturation concentration for all treatments. Marks are the average of three replications. Lines show the estimated DO concentrations by Eq. (3).

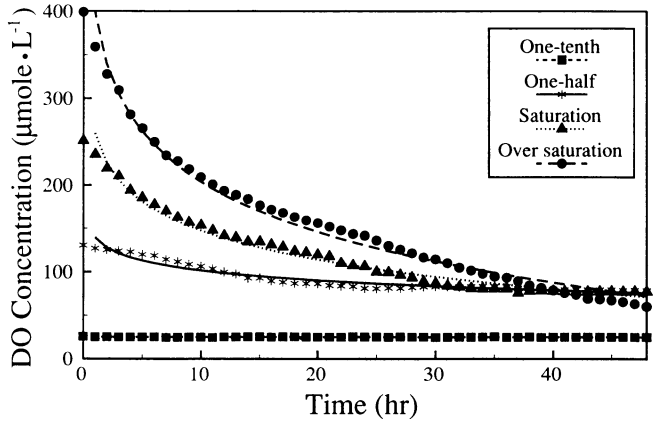

Fig. 3 Time course of DO concentration under various initial DO concentration during a 48-hr measurement period. Plants are at the stage of 26 days after transplanting. Marks are the average three replications. Lines show the estimated DO concentrations by Eq. (3).

Figure 3 shows the changes in DO concentration of the nutrient solution under various initial DO concentration, resulting from the effect of the four plants that were at the growth stage of 26 days after transplanting.

The DO concentrations decreased rapidly with time after the measurements started, and became nearly constant at around 78.2 μmol·liter^{-1} in all treatments except "treatment one-tenth." This suggests that the minimum DO concentration for root respiration of lettuce is around 78.2 μmol·liter^{-1} and below

Table 2 Estimated parameters of the model, β_0^* and β_1 (in μmol·liter^{-1}·hr^{-1}), and the coefficient of determination, R^2 of Eq. (3).

Parameters and R^2 [z]		Over saturation	Saturation	One-half	One-tenth
26D[x]	β_0^*	0.397	0.261	0.116	—[y]
	β_1	−0.083	−0.049	−0.010	—
	R^2	0.985	0.983	0.932	0.073
10D	β_0^*	0.360	0.257	0.100	—
	β_1	−0.028	−0.020	−0.009	—
	R^2	0.974	0.957	0.976	0.066
4D	β_0^*	0.390	0.255	0.141	—
	β_1	−0.023	−0.010	−0.009	—
	R^2	0.974	0.977	0.876	0.072

[z] All parameters are the same as shown in Eqs. (2) and (3).

[y] Not presented because of the low R^2.

[x] Letter D represents days after transplanting.

this concentration, root respiration is greatly obstructed. In practical hydroponic culture using a re-circulation system, DO concentration often becomes lower than this concentration, especially in the last stages of the culture period. Considering that the saturated DO concentration is as low as 263 μmol·liter^{-1} at 23°C, the range of DO concentration for lettuce to grow without oxygen deficiency is very narrow. This also suggests that enrichment of DO is necessary to maintain vigorous root respiration in hydroponics.

In hydroponic systems, aeration is usually performed in storage tanks. Bubbling, agitation or other oxygn-enrichment facilities are installed to maintain the DO concentration near the saturation concentration. However, the rapid decrease in the DO concentration as shown in Fig. 3 suggests that only raise the initial DO concentration are insufficient in providing enough oxygen for the whole growing period. Though the nutrient solution is oxygen-rich in the storage tanks, its concentration may decrease while the nutrient fluid passes through the root respiration. This could explain the nonuniform DO concentrations in the NFT beds.[8]

In "treatment over-saturation," DO concentration decreased very rapidly, and about five hr after the experiment started, it reached to the same DO concentration in "treatment saturation." This suggests that the method of increasing the aerial oxygen partial pressure, which is well established in microbial bioreactors, is not an effective method to improve oxygen environments in hydroponics. Furthermore, considering the poor airtightness of the storage tanks in practical cultures, both maintaining the high oxygen concentration in the gas phase of storage tanks and maintaining the nutrition solution saturated with oxygen are not simple to accomplish.

The coefficients of the equations, and R^2 values of Eq. (2) are listed in Table 2. The high R^2 values in all treatments except "treatment one-tenth" shows that this regression equation well explains the change of DO concentration. The R^2 value for "treatment one-tenth" was much lower than the R^2 values of other treatments, because all treatments were analyzed by the same logarithmic equation though "treatment one-tenth" had a constant DO concentration.

Root respiration and DO concentration

Figure 4 shows the relationship between the rate of root respiration derived from Eq. (4) and the DO concentration in the measurements with the plants

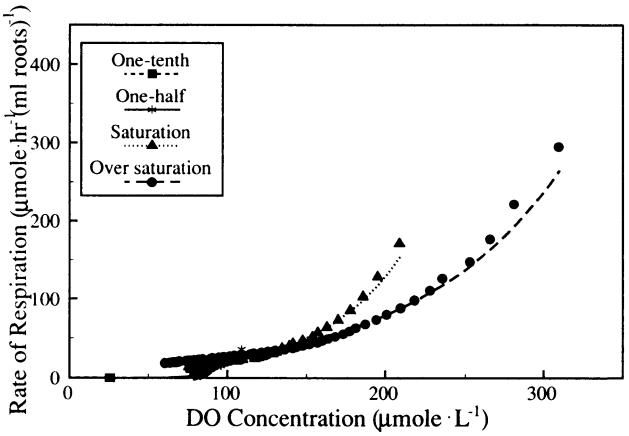

Fig. 4 Relationship between the rate of root respiration and the DO concentration. Plants are at the stage of 26 days after transplanting. Marks are the average of three replications. Lines show the estimated rate of root respiration by Eq. (5).

26 days after transplanting. The rate of root respiration was presented as a function of DO concentration over time using Eq. (5). The rate of root respiration for "treatment one-tenth" was constant, and its value was nearly zero. The rates of root respiration of other treatments were expressed with exponential curves. All treatments had high regression coefficients of determination for the relationship between the rate of root respiration and DO concentration (Table 3). This shows that the rate of root respiration is determined by the concentration of DO around the root system. The rate of root respiration observed in the beginning period was higher than the estimated rate. A possible factor in the initial high rate of root respiration is the stress from transplanting into the measuring box. The different DO concentrations in measuring boxes from those in the DFT beds where the plants were prepared, were thought to be the stress for plants, too.

The rate of root respiration for "treatment over-saturation" kept increasing with the higher DO concentration than the saturation concentration, but it became smaller than that for "treatment saturation" in lower DO concentration regions. This suggests that the greater root respiration with higher DO concentration caused much consumption of metabolites in roots and much accumulation of CO_2 both in roots and in nutrient solution, as well as the decrease of rate of root respiration for "treatment over-saturation" was brought on as these results. Furthermore, this process resulted in the different rates of root respiration calculated for "treatment saturation" from that for "treatment over-saturation" at the same DO concentration.

For DO concentrations in the range from 190 to 230 μmol·liter^{-1} which are usually observed in well aerated hydroponic beds, the rate of root respiration of lettuce ranged from 2.9 to 6.7 μmol·hr^{-1}·(ml roots)$^{-1}$ at 23°C.

Table 3 Estimated parameters of the model, β_2 and β_3, and the coefficient of determination, R^2 of Eq. (5).

Parameters and R^2 [z]		Over saturation	Saturation	One-half	One-tenth
26D[x]	β_2	8.582	2.952	0.002	—[y]
	β_3	0.011	0.019	0.091	—
	R^2	0.990	0.987	0.900	0.050

[z] All parameters are the same as shown in Eq. (5).
[y] Not presented because of the low R^2.
[x] Letter D represents days after transplanting.

Root growth and DO concentration

Tables 4 and 5 show that there were larger root growth and much greater amounts of transpiration during the 48 hr of measurement in "treatment saturation" than in other treatments. Root growth and amounts of transpiration were small in "treatment one-half" and "treatment one-tenth," both of which had the lower rate of root respiration. This suggests that low DO concentration forces the rate of root respiration to be low, and eventually decreases the root growth and amount of transpiration. These results support the report that under low DO concentration, root growth is delayed[15] and water stress increases.[16,17] In "treatment over-saturation" which the initial rate of root respiration was greatest, root growth and transpiration were retarded. It is considered that the higher root respiration caused much consumption of metabolites in roots and it retarded the root growth and transpiration. The root color changed to dark brown in "treatment over-saturation."

This suggests that the method of increasing the aerial oxygen partial pressure be not an effective method to improve oxygen environments in hydroponics.

CONCLUSION

The minimum DO concentration for root respiration of lettuce was around 78.2 μmol·liter^{-1}. DO concentrations lower than this value often occur in hydroponic cultures using re-circulating nutrient solution.[7,8] This indicates that enrichment of

Table 4 Effects of initial DO concentration on root growth. The root growth per plant[z] was represented by the increase in root volume during the 48-hr culture period in the measuring box.

Growth stages	Over saturation (ml)	Saturation (ml)	One-half (ml)	One-tenth (ml)
26D[x]	0.298±0.092[y]	0.382±0.097	0.210±0.073	0.043±0.012
10D	0.057±0.020	0.061±0.021	0.054±0.010	0.031±0.010
4D	0.031±0.005	0.033±0.005	0.017±0.003	0.008±0.002

[z] Average root volume estimated by Eq. (1) was subtracted from the root volume of each plant. Volume measurements were taken after the 48-hr culture period in the measuring box.

[y] Standard errors are shown next to the means.

[x] Letter D represents days after transplanting.

Table 5 Effects of initial DO concentration on transpiration. The amount of transpiration was represented by the decrease in average volume of nutrient solution per hour during the culturing of four plants for 48 hr in the measuring box.

Growth stages	Over saturation (ml·hr^{-1})	Saturation (ml·hr^{-1})	One-half (ml·hr^{-1})	One-tenth (ml·hr^{-1})
26D	5.59±0.28[z]	6.59±0.59	6.07±0.39	4.56±0.26
10D	0.49±0.14	0.58±0.21	0.54±0.23	0.41±0.06
4D	0.22±0.10	0.27±0.09	0.25±0.140	0.19±0.04

[z] Standard errors are shown next to the means.

DO is necessary for maintaining vigorous root respiration in hydroponics. The rate of root respiration was expressed as a function of DO concentration, and increased as the DO concentration of the nutrient solution increased. For DO concentrations in the range from 190 to 230 μmol·liter^{-1} which are usually observed in well aerated hydroponic beds, the rate of root respiration of lettuce ranged from 2.9 to 6.7 μmol·hr^{-1}·(ml roots)$^{-1}$ at 23°C.

The method of increasing the aerial oxygen partial pressure is a well-established method for improving aeration in microbial bioreactors.[18] To test the possibility of applying this method to the hydroponic system, "treatment over-saturation" was prepared and analyzed. In this treatment, however, the root color changed to dark brown, and the root growth and transpiration was retarded. This suggests that the method of increasing aerial oxygen partial pressure be not an effective method of improving oxygen environments in hydroponics. The rate of root respiration was highest in "treatment saturation" and "treatment over-saturation." In this treatment, greater root growth and much greater amounts of transpiration were attained than in other treatments.

The present experiment should result in some beneficial information for developing models for root respiration and oxygen transfer into the roots and it would be helpful for understanding the phenomena of oxygen deficiency and non-uniformity of DO concentration on the hydroponic beds. Data about the rate of root respiration would be used in a series of future studies on flow characteristics and the concentration of DO in hydroponics, and on control methods to improve the root environment for hydroponic plant production.

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〈和文抄録〉

養液の溶存酸素濃度とレタスの根呼吸速度

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レタスの根呼吸を測定するため根圏が密閉された水耕システムを製作した．定植後4日，10日，26日目のレタスを，48時間生育させながら溶存酸素濃度の変化をモニタリングした．各試験区において，溶存酸素濃度の変化から，根呼吸に必要な溶存酸素の臨界値と根呼吸速度を求めた．

定植後26日目のレタスの根呼吸のための溶存酸素濃度の臨界値は，7.82×10^{-5} mol·liter^{-1} であった．また，根の呼吸速度は，溶存酸素濃度の関数として表現できることが明らかになった．健全に植物が生育できる溶存酸素濃度の範囲である，$19\sim23\times10^{-5}$ mol·liter^{-1} でのレタスの根呼吸速度は，養液温度23°C で，$0.29\sim0.67\times10^{-5}$ mol·hr^{-1}·(ml roots)$^{-1}$ であった．飽和溶存酸素濃度区で，呼吸速度がもっとも高く，根生長量および蒸散量が最大となった．しかし過飽和溶存酸素濃度区では，養液成分の酸化，根の褐変などが生じ，根の生育が低下した．