二酸化炭素濃度と葉温の上昇がトールフェスク(Festuca arundinacea Schreb.)の光合成速度に及ぼす影響

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Effects of Increasing CO_2 Concentration and Leaf Temperature on the Photosynthesis of Tall Fescue (*Festuca arundinacea* Schreb.)

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Synopsis

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Carbon dioxide (CO_2) is well known to be a "greenhouse gas" which is capable of causing significant climatic changes. The optimum ranges in the growing area of grass species will likely shift as a result of climatic changes, and there will be corresponding changes in the vegetation zones here in Japan. It is therefore necessary to determine the optimum range for each species that will grow in the new vegetation zones expected from the result by the climatic changes. We measured the effect of increasing CO_2 concentration and leaf temperature on the net photosynthetic rate (Pn) of tall fescue.

Tall fescue (*Festuca arundinacea* Schreb. cv. Nanryo) was grown in 1/5000a Wagner pots in two phytotrons with inflow CO_2 concentrations of 350 ppm and 700 ppm. Pn was measured under different environmental conditions. Six different leaf temperatures (15°, 20°, 25°, 30°, 33° and 35℃) and 8 different CO_2 concentrations (0, 30, 100, 200, 350, 500, 700 and 1,000 ppm) were set for each tiller (grown in CO_2 concentration of either 350 or 700 ppm). The results showed that Pn increased with CO_2 concentration below 500 ppm at each temperature, and decreased with CO_2 concentrations above 700 ppm at leaf temperatures of 15, 20 and 25℃. The rate of decrease in Pn of tillers grown in 350 ppm was higher than that of tillers grown in 700 ppm.

In order to examine the effect of doubling CO_2 concentration, the Pn was regressed by the quadratic of leaf temperature. The effect of the increase in CO_2 concentration on the relative photosynthetic ratios was calculated for each temperature, and the relationship between the relative photosynthetic ratio and leaf temperature was examined. The relative ratio was found to increase with rising leaf temperature. According to this relation, both of the examined parameters expected to increase with global warming, *i.e.* temperature and CO_2 concentration, would have positive effects on the growth of tall fescue.

Key words : Carbon dioxide, Photosynthesis, Tall fescue, Temperature.

Introduction

It has recently been predicted that the greenhouse effect will dramatically change global weather patterns ; air temperature, in particular, is expected to rise in the coming years. Carbon dioxide (CO_2) is well known to be a "greenhouse gas" which is capable of causing significant climatic changes. In 1994, the CO_2 concentration at Mauna Loa, Hawaii, was 358 ppm. This level is forecast to rise to between 450 and 1,000 ppm by the end of this century[22]. The optimum ranges in the growing area of grass species will likely shift as a result of climatic changes[5,17], and there will be corresponding changes in the vegetation zones here in Japan. It is therefore necessary to determine the optimum range for each species that will grow in the new vegetation zones expected from the result by the climatic changes.

Climatic changes due to greenhouse gases will directly affect plant growth in two ways : through the elevated temperatures and increased CO_2 concentrations. It is easy to predict that the rise in temperature will lead to an increase in the area of pasture-land where tropical grasses can be cultivated. On the other hand, the effect of rising CO_2 concentration on plants is difficult to predict depending on species, although it has already been examined in some species[7,9]. In general, rising CO_2 concentration increases the productivity of C_3 plants by direct CO_2 enrichment[14,15,19], while the effect on C_3 plants is more than that on C_4 plants[8,13]. Unfortunately, detailed research has been limited to some species[5,14,15]. It is still necessary to evaluate the effect of changes in CO_2 concentration and temperature on each grass species, in order to forecast the change in productivity of many grass species expected to be accompanied by climatic changes.

In previous studies[14,15] we examined photosynthesis of perennial ryegrass (*Lolium perenne* L.) and

orchardgrass (*Dactylis glomerata* L.), temperate grass species widely utilized in Japan, to evaluate the effects of increasing CO_2 concentration and rising temperature. It was showed that both factors have positive effects on photosynthesis. Tall fescue (*Festuca arundinacea* Schreb.) is another temperate grass, which is widely utilized for grazing in Japan. We measured the effect of doubling CO_2 concentration and rising temperature on the net photosynthetic rate (Pn) of tall fescue leaves.

Materials and Methods

1. Cultivation of the Sample Species

Tall fescue (*Festuca arundinacea* Schreb. cv. Nanryo) was grown in 1/5000a Wagner pots in two phytotrons with inflow CO_2 concentrations of either 350 ppm or 700 ppm. The grass was grown at a temperature of 25℃ in daytime and 20℃ in nighttime. Slow release fertilizer, containing equal amounts of nitrogen, phosphorus and potassium, was applied to each pot, both at the initial sowing and again at the cutting, so as to give an amount of each element equivalent to 0.5 g/pot.

2. Effects of CO_2 concentration and leaf temperature

CO_2 response curve of the Pn was measured with a portable photosynthesis system (LI-6400P, Li-Cor Co. Ltd., USA) under different environmental conditions when leaves were of substantial size. Six different leaf temperatures (15°, 20°, 25°, 30°, 33° and 35℃) and 8 different CO_2 concentrations (0, 30, 100, 200, 350, 500, 700 and 1,000 ppm) were set for each CO_2 concentration (grown in either 350 ppm or 700 ppm). Light intensity was constantly 1,000 μmol photons m^{-2} s^{-1} and relative humidity was kept in between 60 and 80% during measurement. The measurement was performed three times for each condition on the youngest fully expanded leaves.

The effects of rising temperature and CO_2 concentration were examined from the relationships between CO_2 concentration and Pn of each temperature.

3. Complex effects of CO_2 concentration and leaf temperature

The effect of CO_2 concentration on the relationship between leaf temperature and Pn for two different tillers (grown in either 350 ppm or 700 ppm CO_2) was measured at 6 temperatures (15°, 20°, 25°, 30°, 33° and 35℃). Changes in the Pn and optimum leaf temperature due to the doubling of CO_2 concentration were then examined. In addition, the relative ratio of Pn at 700 ppm to that at 350 ppm CO_2 was calculated for a given temperature, and the effects of doubling CO_2 concentration from 350 ppm to 700ppm were examined from the relationship between leaf temperature and Pn of each CO_2 concentration, in order to assess the effects of global warming.

Results

1. Effects of CO_2 concentration and leaf temperature

The relationships between CO_2 concentration and Pn with each leaf temperature are shown for growing condition of 350 ppm CO_2 in Fig. 1 and that of 700 ppm in Fig. 2.

Both figures show that Pn increases with CO_2 concentration below 500 ppm at each temperature, and decreases with CO_2 concentration above 700 ppm at leaf temperatures of 15, 20 and 25℃. Both figures also show that leaf temperature have little effect on Pn at CO_2 concentrations below 350 ppm, and that Pn in-

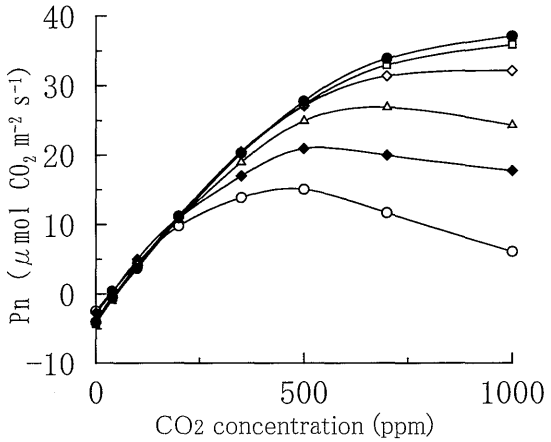

Fig. 1. Relationship between CO_2 concentration and net photosynthetic rate (Pn) of tall fescue at six different leaf temperatures grown in 350 ppm CO_2. (○ : 15℃, ◆ : 20℃, △ : 25℃, ◇ : 30℃, □ : 33℃, ● : 35℃)

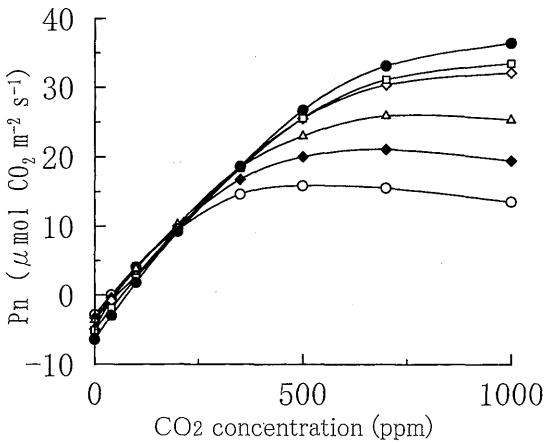

Fig. 2. Relationship between CO_2 concentration and net photosynthetic rate (Pn) of tall fescue at six different leaf temperatures grown in 700 ppm CO_2. (○ : 15℃, ◆ : 20℃, △ : 25℃, ◇ : 30℃, □ : 33℃, ● : 35℃)

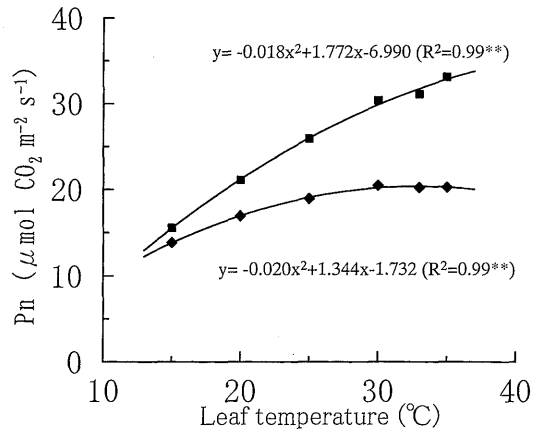

Fig. 3. Relationship between leaf temperature and net photosynthetic rate (Pn) of tall fescue grown in two different concentrations CO_2. (◆ : 350 ppm, ■ : 700 ppm)

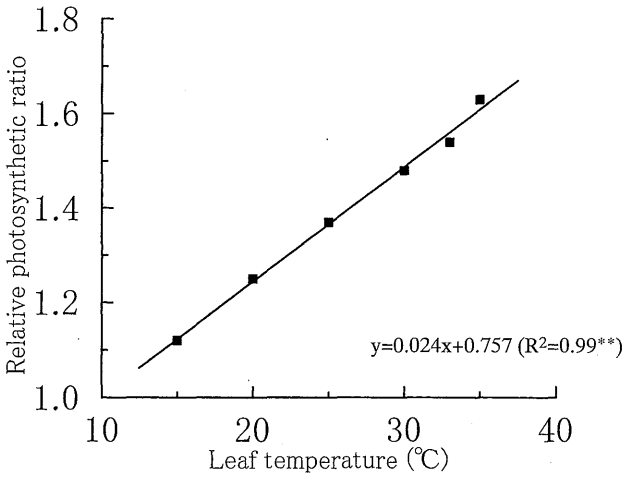

Fig. 4. Relationship between leaf temperature and relative photosynthetic ratio at 700 ppm CO_2 to that at 350 ppm CO_2. ** : $p<0.01$.

creased with leaf temperature above 500 ppm. The rate of increase decreased with increasing leaf temperature.

At low temperatures, the rate of decrease of Pn in tillers grown in 350 ppm was higher than that of tillers grown in 700 ppm. At a leaf temperature of 20℃, tillers grown in 350 ppm have a Pn peak at 500 ppm, but those grown in 700 ppm have a peak at 700 ppm. There is little difference between both figures above 30℃.

2. Complex effects of CO_2 concentration and leaf temperature

The relationships between leaf temperature and Pn for two different tillers (grown in either 350 ppm CO_2 or 700 ppm CO_2) were compared using the data obtained by the above methods.

The effect of the increase in leaf temperature on the Pn at 350 ppm and 700 ppm CO_2 are calculated (Fig. 3.) and the Pn were regressed by the quadratics of leaf temperatures as follows with the coefficients of determination at 0.99 (significant at the 1% level) :

$y_{350} = -0.020\,x^2 + 1.344\,x - 1.732$ ($N=6$, $R^2=0.99^{**}$)

$y_{700} = -0.018\,x^2 + 1.772\,x - 6.990$ ($N=6$, $R^2=0.99^{**}$)

where y_i is the Pn (μmol CO_2 $m^{-2}s^{-1}$) at a CO_2 concentration of i ppm and x is the leaf temperature (℃).

If the peaks of these regression curves are assumed to be the optimum leaf temperatures, the value at 350 ppm is about 33℃ and that at 700 ppm is outside the range of measurement.

In order to assess the effects of global warming, the effect of the increase in CO_2 concentration on the relative photosynthetic ratio at 700 ppm to that at 350 ppm was calculated for each temperature and the results were related positively with the rise in leaf temperature (Fig. 4). The relationship between leaf temperature and relative photosynthetic ratio was regressed as follows with the coefficient of determination at 0.99 (significant at the 1% level) :

$y = 0.024\,x + 0.757$ ($N=6$, $R^2=0.99^{**}$)

where y is the relative photosynthetic ratio and x is the leaf temperature (℃).

This expression shows that Pn of tall fescue is increased by two factors : increases in CO_2 concentration and rising temperature. According to this equation, when the CO_2 concentration increases, a rise in leaf temperature further accelerates the Pn of tall fescue.

Discussion

1. Effects of CO_2 concentration and leaf temperature

Pn increases with CO_2 concentration below 500 ppm at each temperature studied, and decreases with CO_2 concentration above 700 ppm at leaf temperatures of 15, 20 and 25℃. Fig. 1 and Fig. 2 show that the effects of leaf temperature on Pn were small at CO_2 concentrations below 350 ppm, and that Pn increased with leaf temperature above 500 ppm. The rate of increase decreased with increasing temperature. At a CO_2 concentration of 350 ppm, close to the present atmospheric concentration, Pn increases with leaf temperature below 30℃. These results suggest that high CO_2 concentration increases the dependence of photosynthesis on leaf temperature similar with the case of perennial ryegrass[14]. It is clear that the increase in CO_2 concentration increased the Pn and extended the optimum range of leaf temperature. Therefore, CO_2 concentration rather than leaf temperature was hypothesized to limit the photosynthetic ability of tall fescue at high temperature under current climatic conditions.

Comparing the two figures in terms of the decrease of Pn at low temperatures, the rate of decrease of Pn

of tillers grown in 350 ppm was higher than that of tillers grown in 700 ppm. At a leaf temperature of 20℃, tillers grown in 350 ppm have a Pn peak at 500 ppm, but those grown in 700 ppm have a peak at 700 ppm. These results show that one cannot determine whether the increase of CO_2 concentration will have a positive or a negative effect on photosynthesis without specifying the temperature condition, and suggest that tillers acclimatize to an environment with high CO_2 concentration and exhibit higher photosynthetic ability at higher CO_2 concentrations.

2. Complex effects of CO_2 concentration and leaf temperature

Plant species that have been cultivated under doubled CO_2 concentration for a long time differ from each other in terms of changes in Pn. Various species exhibit higher[3,4,13,18], similar[1,12] and lower[2,17] Pn. It has been reported that the Pn of perennial ryegrass[14] and orchardgrass[15] increased between 15 and 35℃ under doubled CO_2 concentration. The present study has shown that Pn of tall fescue have increased at every temperature considered, although the extent of the increase differed depending on the temperatures. Other grass species may differ in their response to changes in CO_2 concentration.

The optimum leaf temperatures calculated from regression curves (Fig. 3) at 350 ppm and at 700 ppm were about 33℃ and out of range respectively. These results are consistent with other reports[5,10,11,16,21] that the optimum leaf temperature of C_3 plants rises with increases in CO_2 concentration.

The relative photosynthetic ratio at 700 ppm CO_2 to that at 350 ppm CO_2 was regressed by leaf temperature. At a leaf temperature of 20℃, the relative photosynthetic ratio is calculated at 1.24 by the regression equation. This value is close to the value of 1.2 for orchardgrass[15] and lower than the value of 1.45 for perennial ryegrass[14]. However, it is considerably higher than the values for C_4 plants (1.15 for maize[20], and 1.18 for bahiagrass[13]).

In conclusion, both of the examined parameters expected to increase with global warming, *i.e.* temperature and CO_2 concentration, would have positive effects on the growth of tall fescue.

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要　　旨

佐々木寛幸・福山正隆*・尾上桐子・須山哲男・小路　敦（2002）：二酸化炭素濃度と葉温の上昇がトールフェスク（*Festuca arundinacea* Schreb.）の光合成速度に及ぼす影響．日草誌 **48**, 12-16，畜産草地研究所（329-2793 栃木県那須郡西那須野町千本松 768），*九州大学農学部（812-8581 福岡市東区箱崎 6-10-1）

地球温暖化の要因の1つとして知られる CO_2 濃度の上昇に伴い，わが国においても各草種の生育適地が変化する可能性があるため，温暖化に対応した草種選定が必要となる。本報では，寒地型牧草のトールフェスクについて，CO_2 濃度と葉温の上昇が光合成速度に及ぼす影響を検討した。

CO_2 濃度を 350 ppm 及び 700 ppm に設定した2つのバイオトロンで生育したトールフェスクの光合成速度を8通りの CO_2 流入濃度（0，30，100，200，350，500，700，1,000 ppm），6通りの葉温（15，20，25，30，33，35℃）で計測した結果，CO_2 濃度 500 ppm までは，いずれの葉温においても，CO_2 濃度の増加に伴い光合成速度も上昇したが，700 ppm 以上では，葉温 25℃ 以下で CO_2 濃度の増加に伴い光合成速度が低下した。その低下程度は，350 ppm で生育した株の方が 700 ppm で生育したものよりも大きかった。

生育及び計測時の CO_2 濃度を 350 ppm 及び 700 ppm とした場合の葉温と光合成速度の関係を葉温の2次式で回帰した結果，CO_2 濃度の倍増に伴い生育適温が上昇することが示された。両者の比を光合成速度の相対倍率として葉温ごとに求め，葉温の1次式で回帰した結果，CO_2 濃度及び葉温の上昇によりトールフェスクの光合成速度が高まることが明らかになった。

キーワード：温度，光合成，トールフェスク，二酸化炭素．