

## Effects of Elevated CO<sub>2</sub> and Temperature on Seedling Emergence of Herbs in a Japanese Temperate Grassland

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**ABSTRACT:** To understand the effects of elevated CO<sub>2</sub> concentration and temperature on seedling emergence of seven herbaceous species, the seedling emergence was monitored between November 1997 and May 1998 using a temperature gradient chamber and a CO<sub>2</sub>-temperature gradient chamber. Experiment was conducted under current ambient condition (Control plot), 2°C-warmed condition with ambient CO<sub>2</sub> (T2 plot), 4°C-warmed condition with ambient CO<sub>2</sub> (T4 plot), and 4°C-warmed condition with 1.8 fold of ambient CO<sub>2</sub> (CT4 plot). Species tested in this study were *Digitaria adscendens*, *Echinochloa crus-galli*, *Panicum bisulcatum*, *Setaria viridis*, *Oenothera biennis*, *Andropogon virginicus*, and *Imperata cylindrica*. Each species often dominates in the herbaceous stage of secondary succession in Japan. The mean seedling emergence times for all species were significantly increased to 23.6 and 32.2 d in the T2 and T4 plot compared to the Control plot, respectively. The most sensitive and insensitive species in seedling emergence time in T2 plot were *O. biennis* and *D. adscendens*, respectively, and those in the T4 and CT4 plot were *I. cylindrica* and *D. adscendens*, *E. crus-galli* and *A. virginicus*, respectively. All experimental species showed no significant difference in the seedling emergence rate between treatments except for *O. biennis* and *I. cylindrica*. *O. biennis* showed a great decrease in the seedling emergence rate from 83.3% in the Control plot to 38.0%, 14.7%, and 29.3% in the T2, T4, and CT4 plot, respectively. Elevated CO<sub>2</sub> had very little effect on the seedling emergence. From these observations, it is expected that increased temperature would greatly advance the vegetative recovery time after disturbance through the advancement of seedling emergence time.

**Key Words:** CO<sub>2</sub>-temperature gradient chamber, Global warming, Secondary succession, Seedling emergence, Species composition, Temperature gradient chamber

### INTRODUCTION

Climate change, caused by the greenhouse effect, is expected to have major impact on northern vegetation by exposing plants to alteration of environmental factors such as elevated CO<sub>2</sub> along with increased temperature. Large vegetation changes are expected at mid- and high-northern latitudes because alteration of climate is predicted to be greater in late autumn and winter than in summer in this area (Kellogg and Zhao 1988, Schlesinger and Zhao 1989, Gates *et al.* 1992, Greco *et al.* 1994). Also, the fact that northern vegetation is highly correlated with temperature supports this prediction. In these areas, plant growth is suppressed by low temperature during the period of late autumn to early spring. Therefore, plants in low temperature season may benefit from the increased temperatures. For example, reduced freezing and chill-

ing damage may enhance survivorship during a cold period, and advanced timing of seed germination, seedling emergence and bud burst may extend growing period. Seedling emergence of many species would be seriously affected by increasing temperature, because temperature is one of the important factors regulating germination. However, some plants may be harmed by increased temperature. In particular, many species in grassland have a particular temperature range for emergence, and emergence rate is determined by temperature. This sensitivity to temperature limits emergence to particular times of the year (Bewley and Black 1982). For example, a high proportion of species—probably the majority of non-tropical species—can be released from dormancy when, in the hydrated condition, they experience relatively low temperatures, generally in the range of 1~10°C (Bewley and Black 1985). The chilling requirement ensures

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that germination occurs in spring. Dormancy of the hydrated seed is slowly broken over the winter and this is presumably a means of preventing germination until the end of winter. Important short-term and, possibly, long-term change in plant species composition and dominance of community may be ascribed to the selective action of new climatic conditions at critical life-cycle stages of plants, such stage as seedling emergence.

On the other hand, many early-successional species require fluctuating temperatures and their germination is inhibited by high CO<sub>2</sub> concentration in the soil (Bazzaz 1996). Their germination is sensitive to light, fluctuated temperature, and CO<sub>2</sub> concentration altered by disturbance of the soil. These results indicate the possibility that recruitments for some species will be influenced by increasing CO<sub>2</sub> concentration. Wulff and Alexander (1985) studied the germination of *Plantago lanceolata* and found that increased CO<sub>2</sub> enhanced germination rate and total germination. Although emergence processes play a great role in determining the species composition of communities (Harper 1978), they have been studied much less than the response of plant growth to elevated CO<sub>2</sub>.

The objective of this study is to determine how the elevated CO<sub>2</sub> and temperature affect the seedling emergence of early secondary successional species growing in abandoned fields of Japanese temperate region. In this region, disturbance and recovery are common, and successional change is so prevalent that no population can exist in the same habitat for a long time. If species in this area respond very differently to elevated CO<sub>2</sub> and increased temperature, then competitive hierarchies can change and the process of community organization and ecosystem recovery after disturbance can also change. Therefore, understanding how elevated CO<sub>2</sub> and temperature affect seedling emergence is very important for predicting effects of global warming on the change in species composition. In order to predict change in the dynamics of secondary succession as a consequence of elevated CO<sub>2</sub> and temperature, it is essential to characterize the effect of elevated CO<sub>2</sub> and temperature on key components of plant life history stage such as emergence time and rate.

## MATERIALS AND METHODS

### Experimental conditions

The experiment was conducted using a temperature gradient chamber (TGC, Lee *et al.* 2000) and a CO<sub>2</sub>-temperature gradient chamber (CTGC).

These facilities can simulate global warming condition with the field-like meteorological rhythm following the diurnal and seasonal fluctuations of air temperature and CO<sub>2</sub> concentration.

The TGC and the CTGC were built at the Terrestrial Environment Research Center in the University of Tsukuba (36.1°N, 140.1°E), Japan. They were 2.5 m high, 3 m wide, and 30 m long. The frameworks were covered with 0.15 mm thick UV-transparent polyvinyl film that has 65~87% of transparency to light with 250~700 nm wavelengths.

The air in the chambers was naturally heated by incident solar radiation: the temperature gradient was created by flowing air from an air inlet to an outlet. The ventilation rates of four ventilators installed on the warm end wall of chamber were controlled by a personal computer on the basis of the temperature difference between the inlet and outlet of the chamber, which was set to 5°C difference. In the case of low or no incident solar radiation, oil heater was automatically turned on to maintain the temperature difference (See Lee *et al.* 2000 for details of this system).

In order to create a CO<sub>2</sub> concentration gradient in the CTGC, CO<sub>2</sub> gas was injected at a rate controlled by adjusting an electronic mass-flow controller automatically. Through two longitudinal distribution pipes, the CO<sub>2</sub> was injected by the blower into the chamber evenly throughout that chamber, which creates gradient of CO<sub>2</sub> concentration with the flow of air from the inlet to the outlet. CO<sub>2</sub> concentration fold-difference was manipulated by controlling the amount of CO<sub>2</sub> gas injection (See Lee *et al.* 2001 for details of this system).

Four treatments were prepared in the TGC and the CTGC: current ambient condition, 2°C-warmed condition with ambient CO<sub>2</sub>, 4°C-warmed condition with ambient CO<sub>2</sub>, and 4°C-warmed condition with 1.8 fold of ambient CO<sub>2</sub>, designated as Control, T2, T4, and CT4 plots, respectively.

### Material plants, sowing, and management

Species tested in this study included four summer annuals (*D. adscendens*, *E. crus-galli*, *P. bisulcatum*, and *S. viridis*), one winter annual (*O. biennis*), and two perennials (*A. virginicus* and *I. cylindrica*). Each species often dominates in the herbaceous stage of secondary succession in Japan (Hayashi 1977, Miyawaki 1979). The seeds were collected between June and October 1997 at the agricultural field of Ibaraki, Japan, and stored in the Control plot until the beginning of germination experiment.

On November 20, 1997, 50 seeds for each

species were sown at the depth of 0.3 cm in each pot, which was filled with 0.5 L sand. Each treatment had three replicates. The pots were placed in the plastic vessel of 40 cm wide, 50 cm long and 5 cm high. The pots were exposed under full sunlight and fully irrigated to maintain wet condition through the experimental period. In order to minimize the effect of spatial temperature difference among the pots, the pots were rotated within treatment location (position) every four days. The air and soil temperatures for each treatment were measured from late-autumn to early-summer. The soil temperature was measured at the depth of 0.5 cm in a pot located at the center of the plastic vessel.

Seedling was counted when a shoot was extended about 0.2 cm long and then monitored every 2 days for 193 days from November 20, 1997 to May 31, 1998. Multiple comparisons of mean values within plot were made using the Tukey test (HSD) to determine whether mean values of the dependent variable were significantly different at the 0.05 probability level.

## RESULTS

### Temperature and CO<sub>2</sub> concentration in the treatments

Fig. 1 shows weekly mean value of air temperature, based on every 10-s data set. The air temperature in the Control plot rapidly decreased to 13.5°C for about 50 d from late-November to early-January (Fig. 1a). The air temperature gradually increased from around mid-February to late-May, and it reached about 23°C in the last experimental stage. The global warming conditions along with the seasonal change of the Control plot were clearly simulated in each treatment (Figs. 1a and b). The mean of air temperatures in the Control, T2, T4, and CT4 plots throughout the experimental period were 8.9, 10.8, 13.1, and 13.3°C, respectively.

The soil temperatures were also simulated with increased temperature condition showing diurnal and seasonal fluctuation (Figs. 1b, 2, and 3a). The mean values of soil temperatures during the experimental period were 10.3, 13.3, 15.5, and 15.4°C in the Control, T2, T4, and CT4 plots, respectively. Diurnal changes of soil temperature in each treatment typically indicated field-like meteorological rhythm (Fig. 2).

In the CTGC, the two folds of ambient CO<sub>2</sub> condition at 25 m away from air inlet was maintained at stable condition throughout the experiment period, except for about one month in February (Fig. 1a). The temporary unstable concentration was accounted for the mis-setting

of the mass-flow controller. It was set below the required CO<sub>2</sub> concentration for achieving the 2x position from inlet to reach two folds concentration.

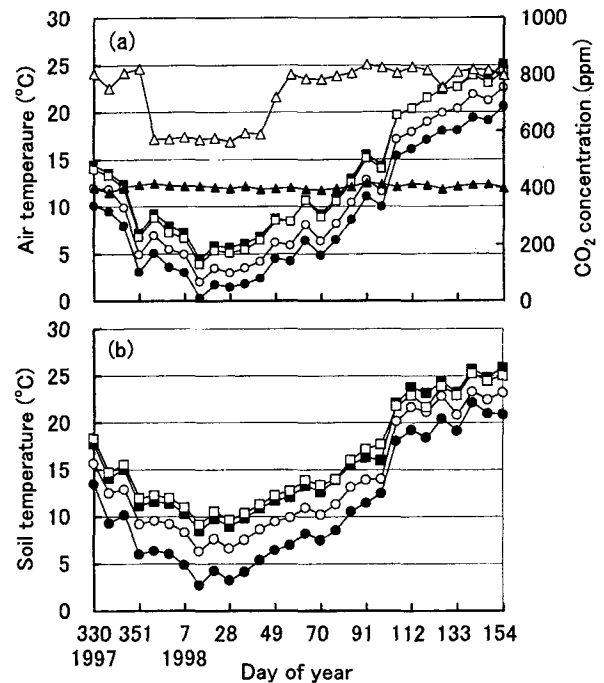


Fig. 1. Weekly means of air temperatures (a) and soil temperatures (b) in each treatment throughout the experimental period. Symbols: ●, Control plot (current ambient condition); ○, T2 plot (2°C-warmed condition with ambient CO<sub>2</sub>); ■, T4 plot (4°C-warmed condition with ambient CO<sub>2</sub>); □, CT4 plot (4°C-warmed condition with 1.8 fold of ambient CO<sub>2</sub>); ▲, ambient CO<sub>2</sub> concentration; △, CO<sub>2</sub> concentration at 25 m away from air inlet in the CTGC.

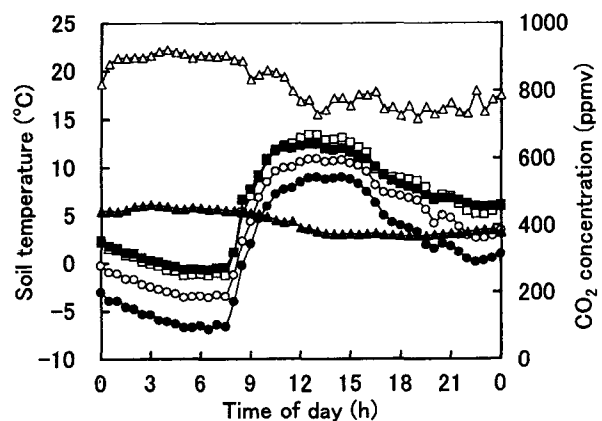


Fig. 2. Diurnal courses of soil temperatures in each treatment and CO<sub>2</sub> concentrations at ambient and 25 m away from air inlet in the CTGC. Symbols are the same as in Fig. 1.

tration than that of inlet. However, the precise CO<sub>2</sub> concentration gradient in the CTGC was achieved after Feb. 10, when the maximum CO<sub>2</sub> supply capacity was readjusted to be higher than the demand. As a consequence, the mean CO<sub>2</sub> concentration at 25 m away from the air inlet was elevated up to  $804.3 \pm 9.2$  ppmv. The mean CO<sub>2</sub> concentrations during the experimental period were 400.7 and 728.3 ppmv at the Control and 25 m away from air inlet in the CTGC, respectively. Diurnal change in CO<sub>2</sub> concentration in the Control plot was shown to be higher in nighttime than that in daytime (Fig. 2). The diurnal fluctuation of CO<sub>2</sub> concentration was also simulated in CO<sub>2</sub> enriched treatment.

### Seedling emergence time

The seedling emergence time (SET) was greatly advanced under increased temperature condition (Table 2). The SET value showed species-specific response. In the T4 plot, the species which showed the most advanced SET was *I. cylindrica* (48.7 d). Also, in the CT4 and T2 plots *E. crus-galli* (28.0 d) and *O. biennis* (30.7 d) showed the most advanced SET, respectively. The least sensitive species to increased temperature were *A. virginicus* (13.3 d), *D. adscendens* (23.3 d), and *S. viridis* (13.4 d) in the CT4, T4, and T2 plots, respectively.

The SET for the Control plot ranged from 132.7 to 158.7 d. As for the T2, T4, and CT4 plots, the SET ranged from 101.3 to 141.3 d, 20.7 to 135.3 d, and 107.0 to 137.3 d, respectively (Table 2). The mean SETs for all species were advanced

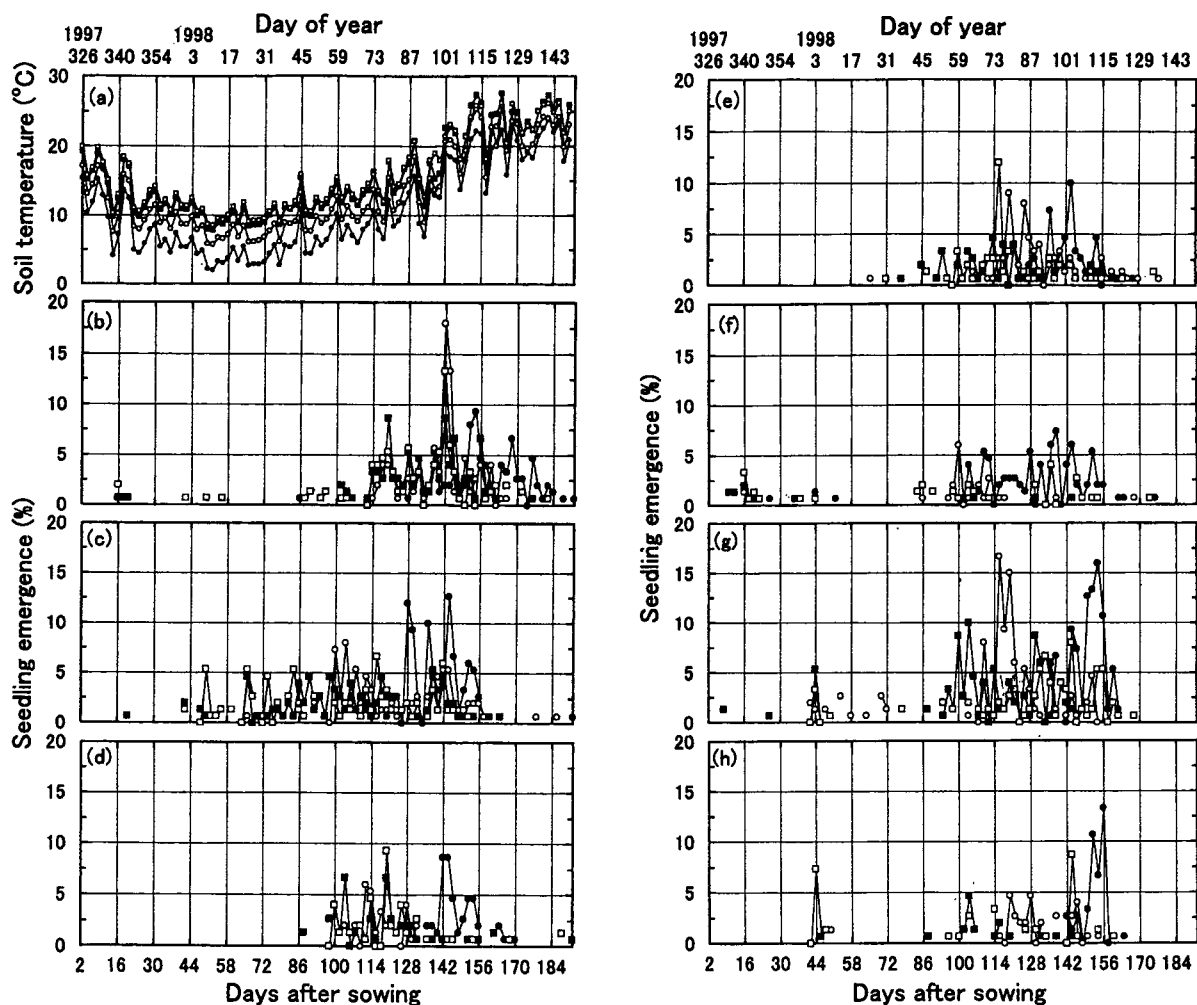


Fig. 3. The relationship between fluctuation of soil temperature (a) and seedling emergence (b-h; b, *Digitaria adscendens*; c, *Echinochloa crus-galli*; d, *Panicum bisulcatum*; e, *Setaria viridis*; f, *Oenothera biennis*; g, *Andropogon virginicus*; h, *Imperata cylindrica*) for seven weed species in elevated CO<sub>2</sub> concentration and temperature. Seedling emergence was enhanced proportionally when soil temperature increased. Symbols are the same as in Fig. 1.

ced to 20.4, 33.3, and 23.9 d in the T2, T4, and CT4 plots compared with the Control plot, respectively.

#### The relationship between seedling emergence and fluctuation of temperature

The seedling emergence rates (SERs) for all species were highly correlated with the irregular fluctuations of soil temperature (Fig. 3). In general, the seedlings emerged in the fluctuation of soil temperature where temperature irregularly increased (Fig. 3), and it was observed that the SERs were low when the soil temperature decreased or sustained low. For example, soil temperature rose to 12.0°C on 108th days after sowing, and to 16.3°C on 114 d when the SER of *D. adscendens* in the T4 plot rose from 0 to 3.3%, (Fig. 3b). Next, soil temperature decreased to 11.9°C on 118 d, and then the SER also decreased to 2.6%. After soil temperature abruptly rose to 17.8°C on 120 d, the SER also rose to 8.7%. The same tendency was observed on 142 d and 144 d when the soil temperatures were as high as 20.7 and 23.0°C, respectively. For *E. crus-galli* on 144 d, *P. bisulcatum* on 142 d and 144 d in the Control plot showed 12.7%, 8.7% and 8.7% of the SER, respectively. As for *S. viridis* on 144 d, *O. biennis* on 144 d and *A. virginicus* on 144 d in the Control plot and *I. cylindrica* on 144 d in the CT4 plot showed 10%, 6.0%, 9.3% and 8.7% of seedling emergence rate, respectively.

With increasing temperature, seedlings emerged for longer duration with low SER compared with the Control plot in which seedlings emerged for shorter duration with high SER. The seedlings of *E. crus-galli* emerged mainly from 42 to 164 d in the T4 plot for 122 days, and from 42 to 152 d in the CT4 plot for 110 days. However, in the Control plot, seedling emergence started from 102 to 164 d for 64 days (Fig. 3c). The seedling of *S. viridis* emerged for 76, 88, 64, and 42 days in the T4, CT4, T2, and Control plots, respectively (Fig. 3e). The seedling of *A. virginicus* was also observed for 56, 74, 42, and 32 days in the T4, CT4, T2, and Control plots, respectively (Fig. 3g).

#### Final seedling emergences rate

The final seedling emergence rates (FSERs) also showed the species-specific response to the increased temperature. The FSER of *O. biennis* was significantly decreased ( $P < 0.05$ ) by temperature rise, and it was 83.3, 38.0, 14.7, and 29.3 % in the Control, T2, T4, and CT4 plots, respectively. *I. cylindrica* showed decrease of the seedling emergence from 41.3% in the Control to 22.7% in the T4. Also the FSER of *D. adscendens* was observed to increase to 10.7%, which had no significant differences among treatments. On the contrary, *S. viridis* showed bigger increase in the FSER in T2 plot (68.7%,  $P < 0.05$ ) than in the Control (50.0%). There was no significant diffe

**Table 1.** The seedling emergence rates of seven herbaceous species under elevated CO<sub>2</sub> and temperature conditions. Values are expressed in the mean percentage with standard error. Different superscript letters within a row indicate statistically significant difference at  $P < 0.05$ . Diff. indicates difference between the Control plot and treatment

| Species                       | Control               | T2                    | Diff.   | T4                       |         |
|-------------------------------|-----------------------|-----------------------|---------|--------------------------|---------|
|                               |                       |                       |         | CT4                      | Diff.   |
| <i>Digitaria adscendens</i>   | 80.0±2.0 <sup>a</sup> | 89.3±8.3 <sup>a</sup> | ( 9.3)  | 90.7 ± 8.1 <sup>a</sup>  | (10.7)  |
|                               |                       |                       |         | 90.7 ± 5.0 <sup>a</sup>  | (10.7)  |
| <i>Echinochloa crus-galli</i> | 93.3±4.2 <sup>a</sup> | 92.0±5.3 <sup>a</sup> | (-1.3)  | 91.3 ± 1.2 <sup>a</sup>  | (-2.0)  |
|                               |                       |                       |         | 86.7 ± 5.0 <sup>a</sup>  | (-6.7)  |
| <i>Panicum bisulcatum</i>     | 50.0±7.2 <sup>a</sup> | 33.3±8.1 <sup>a</sup> | (-16.7) | 35.3 ± 5.0 <sup>a</sup>  | (-14.7) |
|                               |                       |                       |         | 39.3 ± 15.3 <sup>a</sup> | (-10.7) |
| <i>Setaria viridis</i>        | 50.0±5.3 <sup>a</sup> | 68.7±7.6 <sup>b</sup> | (18.7)  | 58.7 ± 3.1 <sup>ab</sup> | (8.7)   |
|                               |                       |                       |         | 48.7 ± 1.2 <sup>ab</sup> | (-1.4)  |
| <i>Oenothera biennis</i>      | 83.3±4.6 <sup>a</sup> | 38.0±5.3 <sup>b</sup> | (-45.3) | 14.7 ± 3.1 <sup>c</sup>  | (-68.7) |
|                               |                       |                       |         | 29.3 ± 8.1 <sup>b</sup>  | (-54.0) |
| <i>Andropogon virginicus</i>  | 86.7±7.6 <sup>a</sup> | 93.3±4.2 <sup>a</sup> | (6.7)   | 92.7 ± 5.0 <sup>a</sup>  | (0.6)   |
|                               |                       |                       |         | 78.0 ± 14.0 <sup>a</sup> | (-8.7)  |
| <i>Imperata cylindrica</i>    | 41.3±9.0 <sup>a</sup> | 40.0±4.0 <sup>a</sup> | (-1.4)  | 22.7 ± 11.7 <sup>b</sup> | (-18.7) |
|                               |                       |                       |         | 30.7 ± 3.1 <sup>a</sup>  | (-10.7) |

**Table 2.** The seedling emergence times of seven herbaceous species in the four treatment conditions. The seedling emergence time is defined as the emerged time of 50% of finally emerged seedlings. Values are expressed as the mean days with a standard error. Different superscript letters within a row indicate significant difference at  $P < 0.05$ . Diff. indicates difference between the Control plot and treatment

| Species                       | Control                | T2                      | Diff.   | T4                        |          |
|-------------------------------|------------------------|-------------------------|---------|---------------------------|----------|
|                               |                        |                         |         | CT4                       | Diff.    |
| <i>Digitaria adscendens</i>   | 158.7±6.1 <sup>a</sup> | 141.3±3.1 <sup>b</sup>  | (-17.3) | 135.3 ± 6.4 <sup>b</sup>  | (-23.3)  |
|                               |                        |                         |         | 134.0 ± 5.3 <sup>b</sup>  | (-24.7)  |
| <i>Echinochloa crus-galli</i> | 138.0±5.3 <sup>a</sup> | 120.7±15.1 <sup>a</sup> | (-17.3) | 104.7 ± 2.3 <sup>b</sup>  | (-33.3)  |
|                               |                        |                         |         | 110.0 ± 5.3 <sup>b</sup>  | (-28.0)  |
| <i>Panicum bisulcatum</i>     | 144.7±1.2 <sup>a</sup> | 114.3±1.2 <sup>b</sup>  | (-30.3) | 116.7 ± 4.6 <sup>b</sup>  | (-28.0)  |
|                               |                        |                         |         | 120.0 ± 0.0 <sup>b</sup>  | (-24.7)  |
| <i>Setaria viridis</i>        | 142.7±1.2 <sup>a</sup> | 129.3±1.2 <sup>b</sup>  | (-13.4) | 112.0 ± 2.0 <sup>c</sup>  | (-30.7)  |
|                               |                        |                         |         | 116.0 ± 0.0 <sup>c</sup>  | (-26.7)  |
| <i>Oenothera biennis</i>      | 132.0±4.0 <sup>a</sup> | 101.3±4.0 <sup>a</sup>  | (-30.7) | 20.7 ± 13.6 <sup>b</sup>  | (-111.3) |
|                               |                        |                         |         | 107.0 ± 22.1 <sup>a</sup> | (-25.0)  |
| <i>Andropogon virginicus</i>  | 150.7±4.2 <sup>a</sup> | 119.3±4.2 <sup>b</sup>  | (-31.3) | 114.7 ± 13.6 <sup>b</sup> | (-36.0)  |
|                               |                        |                         |         | 137.3 ± 6.1 <sup>a</sup>  | (-13.3)  |
| <i>Imperata cylindrica</i>    | 152.7±1.2 <sup>a</sup> | 128.0±1.2 <sup>b</sup>  | (-24.7) | 104.0 ± 0.0 <sup>c</sup>  | (-48.7)  |
|                               |                        |                         |         | 128.0 ± 15.1 <sup>b</sup> | (-24.7)  |

rence between the T4 (58.7%) and CT4 (48.7%) plots. *D. adscendens*, *E. crus-galli*, and *A. virginicus* showed around 80% or higher FSER at all plots.

#### The response of seedling emergence to the CO<sub>2</sub> enriched condition

The seedlings in the T4 plot emerged mainly before the winter, while those in the CT4 plot showed emergence around winter and some before or after, uniformly. *I. cylindrica* in the T4 plot resulted in 8% lower seedling emergence rate than in the CT4 plot (Table 1). *A. virginicus* and *I. cylindrica* showed significantly ( $P < 0.05$ ) earlier SETs in the T4 plot than in CT4 plot (Table 2).

### DISCUSSION

Seedling emergence was highly correlated with the irregularly fluctuating soil temperature, suggesting the minimal temperature requirement for germination (Fig. 3). The seedling emergence rates for all species were high when soil temperature was highly increased. Also, the seedling emergence rates remained low as soil temperature decreased. Such tendency was observed more clearly in the Control plot than in increased temperature conditions. Seedlings in the Control plot emerged at the relatively higher rate than

those in increased temperature plots. However, with increasing temperature, seedlings frequently emerged at the lower rate even though it was observed for longer duration than in the Control plot (Fig. 3). As a result, the duration of seedling emergence was lengthened by temperature rise. These results indicate that seedling emergence (or germination) was restrained by low temperature in which phenological development ceases ( $T_{base}$ ) (Garcia-Huidobro *et al.* 1982, Scott *et al.* 1984, Wiese and Binning 1987, Steinmaus *et al.* 2000). In winter as a low temperature season, seeds are disposed under the  $T_{base}$ , which depresses physiological activity of seeds. The period of low temperature restricting the seedling emergence will be greatly reduced under global warming. If the dormancy is broken or vernalization is not required, it will offer more opportunities of emergence to plants under the global warming condition than the current winter. As a result, current seedling emergence time in Northern vegetation will be shifted to winter.

In this study, the seedling emergence times of all experimental species were greatly advanced by increased temperature (Table 2). The seedling emergence times overall were advanced by 23.6 d and 32.2 d in the T2 and T4 plots, respectively (Table 2). These results suggest that the global warming would greatly aid in vegetative

recovery time through advancing seedling emergence time. The duration of cool season restricting photosynthetic activity of plant would also be shortened by the global warming. The growing season would be proportionally elongated as the global warming progresses. Consequently, the elongated possible growing season would result in the increase of annual net primary productivity per unit area, which is one of the most obvious effects from the global warming. The effect of global warming on plant phenology of emergence is expected to be greater in the mid- and high-northern latitude areas because those areas are predicted to show larger increase in temperature than any other areas, and larger increase during winter than summer (Gates *et al.* 1992, Greco *et al.* 1994).

However, the responses of the seedling emergence time to increased temperature showed species-specificity. These differences in species-specificity may be associated with the seed germination response to temperature. The change of the potential activity, such as seedling emergence time, suggests the possibility that species composition of community can be greatly altered by global warming. Generally, the seedlings reaching the soil surface later are likely to be subordinated in the canopy by the earlier emerging species. The earlier emerging species are expected to preoccupy resources, including space, and suppress later emerging seedlings. Therefore, these late recruits are competitively inferior and can suffer much mortality because their earlier-recruited neighbors are already growing (Bazzaz 1996).

In addition to the change of seedling emergence time, the changes of seedling emergence rate due to species-specific property would also become a factor affecting the change of species composition of community in many ecosystems (Kegode *et al.* 1998). In this study, *I. cylindrica* and *O. biennis* showed significant increase in the seedling emergence rate to the increased temperature while *S. viridis* was decreased. *D. adscendens*, *E. crus-galli*, *P. bisulcatum* and *A. virginicus* were not changed in seedling emergence rate (Table 1). From these results, with global warming, *S. viridis*, *D. adscendens*, *E. crus-galli*, and *A. virginicus* will have more chance in recruitment than in current vegetation or will not change. In contrast, *O. biennis* showed a great decrease in the seedling emergence rate from 83.3% in the Control plot to 38.0%, 14.7%, and 29.3% in the T2, T4, and CT4 plots, respectively. It suggests that *O. biennis* would have great difficulty in establishing population with the temperature increase. Since emergence

processes play a great part in determining the species composition of communities (Harper 1978), poor seedling emergence is a major limitation in establishing population. It supports that some populations may decline and their eventual die-back may occur in many parts of the world (Houghton *et al.* 1990).

Elevated CO<sub>2</sub> had a weak effect on seedling emergence compared with increased temperature (Table 1 and 2). In early-successional fields, CO<sub>2</sub> concentration in the soil is high (Schwartz and Bazzaz 1973), and it inhibits germination of some species in the seed bank. However, in this study, we sowed seeds near the soil surface, where seeds experience lower CO<sub>2</sub> concentration than in the deep soil. At the least, the germination activity of seeds deposited near the soil surface would be affected little by elevated CO<sub>2</sub>. Garbutt *et al.* (1990) found no detectable effect of enhanced CO<sub>2</sub> on timing of emergence and emergence rate in any of *Abutilon*, *Ambrosia*, *Chenopodium*, *Amaranthus* and *Setaria*.

Overall, our results indicate that seedling emergence time will be greatly advanced by global climate change, and it is more sensitive to increasing temperature than elevating CO<sub>2</sub>. The response to increasing temperature is species-specific, and different response would be an important factor that leads to the change of species composition of community.

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#### LITERATURE CITED

- Bazzaz, F.A. 1996. Plants in changing environment. Cambridge University Press, Cambridge, UK, pp. 82-107.
- Bewley, J.D. and M. Black. 1982. Physiology and Biochemistry of Seeds, Vol. 2. Springer-Verlag, Berlin, pp. 199-269.
- Bewley, J.D. and M. Black. 1985. Seeds: physiology of development and germination. Plenum Press, NY, pp. 175-234.
- Garbutt, K., W.E. Williams and F.A. Bazzaz. 1990. Analysis of differential response of five annuals to elevated CO<sub>2</sub> during growth. Ecology 71: 1185-1194.
- Garcia-Huidobro, J., J.L. Monteith and G.R. Squire. 1982. Time, temperature, and germination of pearl millet (*Pennisetum typhoides* S. & H.). J. Expt. Bot. 33: 288-296.

- Gates, W.L., J.F.B. Mitchell, G.J. Boer, U. Cubasch and V.P. Meleshko. 1992. Climate modeling, climate prediction, and model validation, In J.T Houghton, B.A. Callander and S.K. Varney, (eds.). Climate change 1992, Cambridge University Press, Cambridge, UK, pp. 96-134.
- Greco, S., R.H. Moss, D. Vinner and R. Jenne. 1994. Climate Scenarios and Socioeconomic Projections for IPCC WGII Assessment, IPCC, Washington DC, 67 p.
- Harper, J.L. 1978. Population Biology of Plants. Academic Press. London.
- Hayashi, I. 1977. Secondary succession of herbaceous communities in Japan. Jpn. J. Ecol. 27: 191-200.
- Houghton, J.T., G.J. Jenkins and J.J. Ephraums. 1990. Climate Change. The IPCC Scientific Assessment, Cambridge University Press, Cambridge, UK, 365 p.
- Kegode, G.O., R.B. Pearce and T.B. Bailey. 1998. Influence of fluctuating temperatures on emergence of shattercane (*Sorghum bicolor*) and giant foxtail (*Setaria faberi*). Weed Sci. 46: 330-335.
- Kellogg, W.W. and Z.C. Zhao. 1988. Sensitivity of soil moisture to doubling of carbon dioxide in climate model experiments. Part I: North America. J. Clim. 1: 348-366.
- Lee, J.S., T. Usami, T. Oikawa and H.J. Lee. 2000. High performance of temperature gradient chamber newly built for studying global warming effect on a plant population. Korean J. Ecol. 23: 293-298.
- Lee, J.S., T. Usami and P. Oikawa. 2001. High performance of CO<sub>2</sub> temperature gradient chamber newly built for studying global warming effect on a plant population. Ecol. Res. (in press).
- Miyawaki, A. 1979. Vegetation of Japan. Sibuntou, Tokyo.
- Schwartz, D.M. and F.A. Bazzaz. 1973. *In situ* measurements of carbon dioxide gradient in a soil-plant-atmosphere system. Oecologia 12: 161-167.
- Schlesinger, M.E. and Z.C. Zhao. 1989. Seasonal climatic changes induced by doubled CO<sub>2</sub> as simulated by the OSU atmospheric GCM/mixed ocean model. J. Clim. 2: 459-495.
- Scott, S.J., R.A. Jones and W.A. Williams. 1984. Review of data analysis methods for seed germination. Crop Sci. 24: 1192-1199.
- Steinmaus, S.J., T.S. Prather and J.S. Holt. 2000. Estimation of base temperatures for nine weed species. J. Expt. Bot. 51: 275-286.
- Wiese, A.M. and L.K. Binning. 1987. Calculating the threshold temperature of development for weeds. Weed Sci. 35: 177-179.
- Wulff, R.D. and H.M. Alexander. 1985. Intraspecific variation in the response to CO<sub>2</sub> enrichment in seeds and seedlings of *Plantago lanceolata* L. Oecologia 66: 458-460.

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