Effect of Free-Air CO₂ Enrichment on Structures of Weed Communities and CO₂ Exchange at the Flood-Water Surface in a Rice Paddy Field

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Abstract. Biomass and structural changes of weed communities, and CO₂ exchange between the flooding water and the atmosphere were examined in a paddy field under ambient and free-air CO₂ enrichment (FACE). The biomass of planktonic algae was small throughout the experimental period due to the shallow and variable depth of flooding water in the paddy field. Elevated CO₂ slightly increased the biomass of algae, but the increment was not statistically significant. The CO₂ fertilization effect on the biomass of floating weeds (Lemna perpusilla and Spirodela polyrhiza) was 3-fold in August, and 1.6-fold in September in terms of the ability to exhibit vegetative propagation. In contrast, community structures of the paddy weeds (emergent and terrestrial plants) under FACE conditions did not differ from the ambient condition. The CO₂ fertilization effect on the paddy weeds might be reduced by frequent human weeding and/or nutrient limitation by growth of rice plants. CO₂ evolution from the flooding water occurred throughout the entire day under the ambient CO₂ condition, although the CO₂ evolution rate decreased in the daytime. In contrast, under the FACE condition, CO₂ evolution from the flooding water was observed at night and CO₂ absorption from the atmosphere was observed in the daytime. The time course of CO₂ exchange was similar to that of solar radiation. Thus the diurnal pattern is similar to that of photosynthesis of terrestrial plant communities. This suggests that photosynthesis of the free floating weeds and algae in the flooding water is related to the CO₂ exchange between the flooding water and the atmosphere. Moreover, the amplitude in the diurnal cycle of the CO₂ exchange rate was larger under the FACE than under the ambient condition.

Keywords: CO₂ flux, CO₂ fertilization effect, floating weeds, paddy weed community, planktonic algae, rice FACE

1. INTRODUCTION

Since the increase in the emission of carbon dioxide in the atmosphere may become a serious environmental problem world-wide, quantitative studies on the carbon cycle are essential to predict the CO₂-induced warming effect on the earth.
It is predicted that CO₂ concentration will reach twice the present level in the next century (Houghton et al., 1994). Rising CO₂ concentrations can stimulate photosynthesis and growth of a wide range of C₃ plants (Gifford, 1988; Kimball, 1983). Various laboratory experiments using closed chambers have been conducted to evaluate the effects of elevated CO₂ on plant growth. The plant growth was, however, to some degree altered by the chambers themselves (Moya et al., 1997). The microclimate, nutrient conditions, and limited usable area in the chambers can change the plant responses to elevated CO₂. The results or predictions obtained from laboratory experiments should be evaluated under field conditions. In addition to the eco-physiological processes of plants examined in the laboratory experiments, elevated CO₂ could change various environmental conditions, including the carbon cycle and nitrogen metabolism. Increasing carbon input to the soil through increased root growth, root exudation, altered litter quality, and increased soil water use under elevated CO₂ can all affect soil nitrogen transformations and carbon dynamics (Hungate, 1999). In order to evaluate the effects of CO₂ on the ecological and physiological processes under field conditions and on terrestrial ecosystems in the large and long-term scales, a free-air CO₂ enrichment (FACE) system has been developed and used to study the impact of increasing atmospheric CO₂ on various plants and ecosystems. FACE experiments have been conducted in various croplands to study the impact of increasing atmospheric CO₂, such as cotton, wheat and sorghum in the US and Europe (Kimball et al., 1995; Printer, Jr. et al., 1996; Ottman et al., 2001), and even in a forest ecosystem (Norby et al., 2001). A newly designed FACE system using pure CO₂ has been developed and applied to a paddy field in a cool-temperate region in northern Japan for the first time (Okada et al., 2001). Many studies on the effects of elevated CO₂ on the paddy field ecosystem, e.g. photosynthesis and growth of the rice plants (Kim et al., 2001), CO₂ exchange from the water surface (Koizumi et al., 2001), soil microbial biomass, evapotranspiration and so on, have been intensively conducted in the FACE site from 1997. However, few studies were conducted on the effects of elevated CO₂ on weed communities in the paddy field. The changes of weed communities might affect the structure and function of the paddy field ecosystem. The objective of this paper is to clarify the CO₂ fertilization effect on the three different functional types of weed communities in a paddy field, such as planktonic algae, aquatic floating weeds and the other paddy weeds, and to investigate the processes of CO₂ exchange between the water surface and the atmosphere in a paddy field under ambient and FACE conditions, with emphasis on the diurnal and seasonal changes.

2. MATERIALS AND METHODS

2.1 Study site

The study was conducted at a paddy field in the FACE Experimental Site in Shizukuishi, northern Japan (39°40’ N, 141°00’ E, about 200 m a.s.l.), from June 1999 to September 1999. Climatological data (1961–1990) from a nearby
Fig. 1. Experimental design in the paddy. Two levels of CO₂ conditions (AMBI, ambient; FACE, ambient + 200 µmol mol⁻¹) and four blocks were set in a randomized complete block design.

meteorological station at Morioka (39°42′ N, 141°10′ E, 155.2 m a.s.l.) are as follows: annual mean temperature is 9.8°C with seasonality between minimum monthly mean temperature of −2.5°C in January and maximum monthly mean temperature of 23.2°C in August; annual rainfall is 1265 mm and is distributed throughout the year with a minimum of 55 mm in February. Snow coverage is usually 10 to 20 cm from December to March. The study area can be included in the cool-temperate deciduous broad-leaved forest region. The soil is classified as humic Andosol (Kuroboku). The carbon and nitrogen contents in the topsoil (0–1 cm) were 88 (±2.4) mg C kg⁻¹ and 5.8 (±0.22) mg C kg⁻¹, respectively.

2.2 Experimental design

A FACE ring consists of eight CO₂-emitting tubes in an octagonal arrangement (Fig. 1), from which pure CO₂ is sprayed into the air above the plant canopy without use of blowers. The FACE ring measures 12 m across and has a nominal usable area of approximately 80 m², except for a 1 m buffer zone along the inside of the ring. The detailed mechanisms and performance were previously described by Okada et al. (2001). As shown in Fig. 1, the experiment was conducted in a randomized complete block design with two levels of CO₂ concentrations (AMBI: ambient; FACE: ambient +200 µmol mol⁻¹) and four blocks. We used one block to measure the CO₂ exchange rate at the flood water surface including planktonic
algae and free floating weeds, and four blocks to measure the biomasses of planktonic algae and free floating weeds. The average CO₂ concentration was approximately 370 µmol mol⁻¹ in AMBI and approximately 570 µmol mol⁻¹ in FACE.

Seedlings of rice (*Oryza sativa* L. cultivar “Akita-Komachi”) were raised for 29 days at the Tohoku National Agricultural Experiment Station. The seedlings for the AMBI sites were grown in a chamber with ambient CO₂ concentration, and those for the FACE sites were grown in another chamber with CO₂ concentration set at 200 µmol mol⁻¹ higher than ambient. The seedlings were hand-transplanted into the experiment plots on 20 May 1999. The total dry weight biomass of the rice plant was 1723 g m⁻² for FACE and 1499 g m⁻² for AMBI in September. Nitrogen was supplied as ammonium sulphate at the rate of 4 to 12 g N m⁻². For all N levels, 48 g P₂O₅ m⁻² and 15 g K₂O m⁻² were applied. Nitrogen was applied as a basal dressing (63% of the total), at mid-tillering (20%) and at panicle initiation (17%). Fields were flooded throughout all seasons except for 5 days summer drainage in mid-July and 10 days before harvest. Herbicide at 1 kg per 10a (Prosper A, Kumiai Chemical Industry Co., Ltd.) was supplied to the paddy field on 28 May, 1999. The area around the levee in the paddy field was frequently hand weeded.

### 2.3 Measurements of biomass and community structure of weeds

The effect of CO₂ fertilization on the three different functional types of weeds in the paddy field was studied, i.e., planktonic algae in flooding water, aquatic floating weeds on the surface of flooding water which have no fixed roots, and the other paddy weeds which are emergent and terrestrial plants with fixed roots to the paddy soil. The biomass of planktonic algae was measured on 14 July and 10 August by the following procedure. A 1000 ml sample of the flooding water was collected from three places in each experimental site. The sampled water was filtered through a 100 µm nylon mesh to separate zooplankton, and then filtered through glass microfibre filters (Whatman GF/C, Tokyo Roshi, Japan) under reduced pressure to separate the planktonic algae from the soluble fraction. The carbon content of the filters, on which planktonic algae were sedimented, was measured using a CHN analyzer (SUMIGRAPH NC-900, Shimadzu, Japan). The biomass and total coverage of aquatic floating weeds were measured on 11 August and 9 September by the following procedure. A cylindrical frame of 10 cm in diameter was used for these measurements. Coverage was measured at three places in each experimental site and after harvesting to measure the biomass. The harvested plants were dried at 80°C for more than 24h and the carbon content was measured using a CHN analyzer.

For paddy weed measurements, two plots, which were 30 cm × 60 cm in area, were established in each experimental site (except for some sites due to recent weeding) along the path from the levee to the inside of experimental sites (Fig. 1). Floristic composition and community structures were investigated in each plot on 9 September. All the higher plants (except for floating weeds) were measured for maximum plant height (*H* cm) and coverage (*C%*). After the measurements of
community attributes, all plants in each plot were clipped at ground level. They were oven-dried at 80°C for more than 24 h and weighed. The relative dominance (RD) of each species was calculated by the equation, $RD = \frac{H \times C}{\text{sum of } H \times C}$ of all species in a plot. The number of dominant species in each plot was determined by dominance analysis using RD (Ohtsuka, 1999). The diversity index of each plot was calculated using the Shannon-Weaver formulation using RD (Pielou, 1969). The floristic similarity among all plots was subjected to cluster analysis using a Czekanowski similarity index (Kent and Coker, 1992).

2.4 Measurements of CO$_2$ exchange at the flood-water surface

The measurement was conducted in an experimental plot of 9 m$^2$ (3 m $\times$ 3 m) at FACE and AMBI sites. The CO$_2$ exchange rate between the water surface and atmosphere of the experimental field was measured using the open-flow infrared gas analyzer method (OF method; Nakadai et al., 1993). The measurement was conducted at intervals of approximately 4 weeks. Ambient air at the surface of the flooding water was primarily sent to a container for buffering and then well mixed air was passed through the chamber (21 cm in diameter and 13 cm in height) at a rate of 0.6 l min$^{-1}$ at the AMBI experimental site. Air with 570 µmol mol$^{-1}$ CO$_2$ supplied from a cylinder was passed through the chamber at a rate of 0.6 l min$^{-1}$ at the FACE experimental site. Carbon dioxide concentrations in the air being pumped into and withdrawn from the chamber were measured using an infrared gas analyzer (model ZFC, Fuji Electric, Tokyo, Japan) at intervals of 10 minutes for 24 to 36 hours. The four measuring chambers were placed in each experimental plot (3 m $\times$ 3 m) at each measurement time (Fig. 1) and removed at the end of measurement. The chamber was placed between rows in which soil was not compacted by trampling.

Air, water and soil temperatures were measured using a copper-constantan thermocouple (Ninomiya Densen Kogyo, Japan), at the same time as the CO$_2$ exchange measurement. Air and water temperatures were determined at 30 cm above and 2 cm depth below the water surface, respectively, and soil temperature was measured at a depth of 2 cm. The pH of the flooding water was measured using a glass electrode pH meter (HM-7B, Toa, Japan), but the dissolved CO$_2$ in the water was not measured in the present study.

2.5 Statistical analysis

The biomasses and coverage data of planktonic algae and weeds between the FACE and AMBI sites were statistically analyzed using Student’s unpaired t-test.

3. RESULTS AND DISCUSSION

3.1 Biomass of planktonic algae and floating weeds

The biomass of planktonic algae was small throughout the entire experimental period. Elevated CO$_2$ increased the biomass of algae in July and August, but the increment was not significant (Fig. 2a). The biomass was 0.40 mg C l$^{-1}$ under
AMBI sites and 0.49 mg C l⁻¹ under FACE sites in July, and 0.92 mg C l⁻¹ and 1.06 mg C l⁻¹ in August, respectively. The depth of flooding water of the paddy field varied greatly from 0.5 to 11 cm depending on rainfall. However, the mean water depth did not differ between both AMBI and FACE sites over the experimental period (Fig. 2b).

Two species of floating weeds, *Spirodela polyrhiza* and *Lemna perpusilla* occurred in the paddy field. Coverage of *S. polyrhiza* was rather small (Fig. 3a), 0 to 25%, throughout the experimental period compared to *L. perpusilla*. Elevated CO₂ slightly increased the coverage of *S. polyrhiza* in August. *Lemna perpusilla* covered 10 to 35% of flooding water of the paddy field in AMBI sites and 50 to 70% in FACE sites (Fig. 3b). The coverage of *L. perpusilla* greatly increased in FACE sites in both months. The total biomass of the floating weeds increased from August to September (Fig. 3c). The biomass amounted to 806.2 mg C m⁻² under FACE sites and 272.7 mg C m⁻² under AMBI sites in August, and 870.5 mg C m⁻² and 543.7 mg C m⁻² in September, respectively. The biomass was two to three times greater at FACE than AMBI.

Elevated CO₂ slightly increased the biomass of algae though the increment was not statistically significant and the biomass was rather small and varied. The biomass of planktonic algae in flooding water of paddy fields generally varied with time; for example, biomass varied greatly by 0.78 to 5.81 mg l⁻¹ day by day during the growing period in Nagano, central Japan (Kurasawa, 1956). Kurasawa concluded that estimation of the changes of biomass of planktonic algae in paddy fields was difficult due to shallow water and the variation of water depth.

Fig. 2. Biomass of planktonic algae in flooding water (a) and the depth of water (b) in the paddy field in July and August. Superscript letters indicate the results of Student’s unpaired t-test; *: P < 0.1, **: P < 0.01, ns: not significant.
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Depending on rainfall and/or artificial inflow and outflow of water. These effects resulted in the difficulty in detecting a CO₂ fertilization effect (CFE, McMurtrie and Dewar, 1999) on the biomass of planktonic algae in these study sites. Moreover, the lower values of the biomass might be caused by lower metabolic activity of the algae due to the low temperature of the flooding water in northern areas and weak irradiation below the dense floating weeds during the growing period.

The CO₂ fertilization effect on the biomass of the floating weeds, *L. perpusilla* and *S. polyrhiza*, was 3-fold in August and 1.6-fold in September. The increased biomass of floating weeds due to elevated CO₂ concentration has been investigated, e.g. *Azolla pinnata* (Allen et al., 1988a; Idso et al., 1989) and *Eichhormia crassipes* (Roy et al., 1993). The strong CFE on the floating weeds might be attributed to their ability to exhibit a high rate of vegetative propagation. However, CFE of the two floating weeds in this study reduced from August to September, in spite of the high propagation potential. Under FACE conditions, rice plants showed a significant increase of 15% in total dry weight (Toda et al., 2000) and also in leaf area index (Kim et al., 2001). In this case, light conditions under the rice plant canopy in FACE sites decreased, especially in the mature stage. CFE on the floating weeds might be reduced under conditions of light

Fig. 3. Coverage and biomass of the two species of floating weeds on the surface of flooding water in the paddy field in August and September. Superscript letters indicate the results of Student’s unpaired t-test; *: \( P < 0.1 \), **: \( P < 0.01 \), ns: not significant.
limitation by rice plants at maturity in FACE sites in September. Moreover, a long-term exposure to elevated CO$_2$ produces a decline in net photosynthesis and biomass growth due to a feedback inhibition caused by starch accumulation in leaves (Allen et al., 1988a).

3.2 Community structure of paddy weeds

A total of twelve species of paddy weeds appeared in the eleven plots (Table 1). The five species of typical paddy weeds, *Lindernia dubia*, *Scirpus juncoides*, *Ludwigia epilobioides*, *Monochoria vaginalis* var. *plantaginea*, and *Echinochloa crus-galli* var. *oryzoides* were regarded as dominant species. *Lindernia dubia* and *S. juncoides* widely appeared, and in particular, *L. dubia* had more than 20% of relative dominance (RD) in all plots. Only one C$_4$ plant, *E. crus-galli* var. *oryzoides*, appeared in the paddy field.

There were no apparent differences in community attributes of the paddy weeds between FACE and AMBI sites. Community height of FACE sites was slightly greater than that of AMBI sites, but was not statistically significant. Using the dendrogram showing similarity relationships among the eleven plots of paddy weed communities, floristic similarity among the plots was rather high due to the dominance of *L. dubia*. Three clusters were distinguished by the common dominants at the level of 40% similarities. However, each cluster was included in the plots of both FACE and AMBI sites, so there were no floristic differences between the two sites.

The structures and biomass of the paddy weed communities along the path did not differ between FACE and AMBI sites. The CFE on terrestrial weeds was small compared to floating weeds in general, 1.44 for C$_3$ plants and 1.14 for C$_4$ plants (Poorter et al., 1996) in greenhouse experiments. Most of the paddy weed species in the experimental field were C$_3$ plants. The typical C$_4$ paddy weed, *Echinochloa crus-galli* var. *oryzoides*, appeared only in one plot (Table 1). Herbicide treatment greatly suppressed the occurrence of typical paddy weeds such as *E. crus-galli* var. *oryzoides* and *Eleocharis kuroguwai* in this study site (Sekikawa et al., 1998). Moreover, the paddy weeds along the path had been frequently hand weeded, and thus the growing period and species occurrence were also suppressed by artificial weeding. Therefore, the detection of CFE on the paddy weeds was difficult in field conditions compared to that on the floating weeds.

Concerning the structures of weed communities in the natural paddy field, CFE differed according to the functional types of weeds. The biomass of planktonic algae slightly increased in FACE, but the biomass was rather small. Floating weeds were extensively affected by CO$_2$ fertilization in the field conditions, in particular their ability to exhibit vegetative propagation. There was no apparent CFE on the paddy weeds due to the frequent human weeding in the study sites. The changes of weed communities might affect the structure and function of the paddy field ecosystem; e.g. the increment of floating weeds in FACE sites was related to the CO$_2$ fluxes from the water surface (Koizumi et al.,
Table 1. Floristic composition and relative dominance (RD) matrix of paddy weed communities in AMBI (ambient) and FACE (elevated CO₂) conditions.

<table>
<thead>
<tr>
<th>Species</th>
<th>AMBI</th>
<th>FACE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Plot</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>A-1</td>
</tr>
<tr>
<td>Vegetation cover (%)</td>
<td></td>
<td>90</td>
</tr>
<tr>
<td>Above-ground biomass (g m⁻²)</td>
<td></td>
<td>77</td>
</tr>
<tr>
<td><em>Lindernia dubia</em></td>
<td>C₃</td>
<td>20.3</td>
</tr>
<tr>
<td><em>Scirpus juncoides</em></td>
<td>C₃</td>
<td>17.1</td>
</tr>
<tr>
<td><em>Ludwigia epilobioides</em></td>
<td>C₃</td>
<td>13.2</td>
</tr>
<tr>
<td><em>Monochoria vaginalis</em> var. plantaginea_</td>
<td>C₃</td>
<td>48.4</td>
</tr>
<tr>
<td><em>Sagittaria trifolia</em> var. trifolia_</td>
<td>C₃</td>
<td>—</td>
</tr>
<tr>
<td><em>Scirpus sp.</em></td>
<td>—</td>
<td>1.0</td>
</tr>
<tr>
<td><em>Echinochloa crus-galli</em> var. oryzoides_</td>
<td>C₄</td>
<td>—</td>
</tr>
<tr>
<td><em>Veronica peregrina</em></td>
<td>C₃</td>
<td>0.0</td>
</tr>
<tr>
<td><em>Rotala indica</em> var. uliginosa_</td>
<td>C₃</td>
<td>0.0</td>
</tr>
<tr>
<td><em>Eleocharis congesta</em></td>
<td>C₃</td>
<td>—</td>
</tr>
<tr>
<td><em>Deinostema adenocaulon</em></td>
<td>C₃</td>
<td>—</td>
</tr>
<tr>
<td><em>Eriocaulon cinereum</em></td>
<td>C₃</td>
<td>—</td>
</tr>
</tbody>
</table>

* indicates the dominant species in each plot. C₄ plants refers to Okuda and Furukawa (1990).
Long term experiments using the FACE system are needed to elucidate the CFE on paddy field ecosystems.

3.3 Diurnal and monthly changes in CO₂ exchange between the flooding water and the atmosphere

Under the FACE condition, distinct changes in the level of CO₂ exchange occurred with the growth of rice plants. The daytime CO₂ exchange rate showed negative values even in the early stages (July), while the values were positive for nighttime. In other words, CO₂ was absorbed by the flooding water surface in the daytime and released from the water at night. The rate of CO₂ absorption in the daytime was the highest in the later stages, approximately –50 mg CO₂ m⁻²h⁻¹ on August 10, maintaining that value until September. The nighttime CO₂ exchange rate also seemed to change with time. The nighttime rate was relatively low in the early stage of rice growth (ca. 25 mg CO₂ m⁻²h⁻¹ in July). It increased as the crop season progressed and attained the highest value, more than 100 mg CO₂ m⁻²h⁻¹, in August. Thereafter, the nighttime CO₂ exchange decreased with rice growth, reaching the value of approximately 75 mg CO₂ m⁻²h⁻¹ in September. This trend might be related to the seasonal changes of the metabolic activity of soil microorganisms and the soil temperature, as well as to the seasonal change in CO₂ release from the roots of rice plants (dark respiration of rice roots) and from the free floating aquatic weeds and algae.

By contrast, the diurnal cycle of the CO₂ exchange rate under the AMBI condition was different from that under the FACE condition. CO₂ evolution from the water surface occurred throughout the day under the AMBI condition, although the CO₂ evolution rate decreased in the daytime. The rate of CO₂ evolution was close to zero at midday throughout the crop season. However, the nighttime rate was approximately 20 mg CO₂ m⁻²h⁻¹ in July, increasing with time to attain the highest value, ca. 100 mg CO₂ m⁻²h⁻¹, in August. Thereafter, it decreased somewhat with time. On comparing the pattern of the CO₂ exchange rate under the AMBI condition with that under the FACE condition, the amplitude in the diurnal cycle of the CO₂ exchange rate was found to be larger under the FACE condition than the AMBI condition.

The time course of diurnal CO₂ exchange was similar to that of solar radiation. Thus the diurnal CO₂ exchange pattern is similar to that of photosynthesis of terrestrial plant communities. The diurnal pattern of CO₂ exchange could be affected primarily by the photosynthetic ability of the free floating weeds and algae in the flooding water. This suggests that photosynthesis of the free floating weeds and algae in the flooding water is related to the CO₂ exchange between the flooding water and the atmosphere.

Biological processes (photosynthesis and respiration of aquatic plants and soil microbes) will exert a significant influence on CO₂ flux between the atmosphere and the water surface in paddy fields. Uptake of CO₂ through photosynthesis of plants leads to a decrease in the daytime flux, and emission of CO₂ through respiration of plants and soil microbes leads to an increase in the
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The free floating aquatic weeds can directly exchange CO₂ with the atmosphere, through the upper epidermis of leaves (Satake and Shimura, 1983). Moreover, photosynthesis and respiration of free floating aquatic weeds and soil microbes would result in CO₂ exchange through the water with the atmosphere. The significant relationships between daytime CO₂ flux and PPFD (Photosynthetically active Photon Flux Density) indicate that floating weeds and algae play a substantial role in CO₂ uptake. For the same reason, the monthly change is due to the temporal changes in the production or biomass of dominant free floating aquatic weeds and decomposition of soil microbes. The biomass of the free floating weeds (*Lemna perpusilla* and *Spirodela polyrhiza*) increased until August due to relatively favorable light conditions on the flood water surface. Thereafter the rice plant canopy suppressed the growth of the free floating weeds and these biomasses did not increase much. The higher amplitude of the diurnal changes in the later experimental stages indicates increased production and decomposition of soil organic matter. The effects of the algae on daily CO₂ exchange will be small in August and September when the free floating weeds shade the algae growing under water. The free floating weeds with high coverage capture 63–73% of irradiation penetrating into the water (Fig. 3b).

The results of the FACE experiment suggest that increased production of aquatic weeds, particularly free floating weeds, largely leads to increased carbon uptake under elevated CO₂ concentrations. The future influence of aquatic weeds on CO₂ flux across the water surface in rice paddy fields must be predicted by considering the effects of concurrent changes in other environmental variables such as solar radiation and temperature. Global warming may have a positive and/or negative influence on the carbon flux of aquatic weeds. The rising CO₂ concentration may reduce the amount of solar radiation available for the production of aquatic weeds because of increased growth of rice plants. Increased temperature will enhance the photosynthesis of some free floating aquatic weeds, e.g., *Azolla pinnata* (Allen et al., 1988b).

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