A FACE (free-air CO_2 enrichment) study to predict the impacts of atmospheric CO_2 increase on agricultural ecosystems (Abstract of the Interim Report)

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1. Introduction
The projected increase of atmospheric carbon dioxide (CO_2) and climate change will have significant impacts on future agricultural productivity. Warmer climates are generally considered to reduce crop yield: Higher temperatures will shorten crop growth duration that will limit the biomass production. Heat and water stresses are more likely to occur under warmer climates in the future: This can lead to severe damages on the reproductive organs that are generally of significant importance for economic yield. On the other hand, the elevated atmospheric CO_2 will promote growth and yield via increasing photosynthetic rates. The net change of the crop productivity will depend on the extents of these counteracting effects of future climates, and the magnitude and even the direction of the change will be subject to an uncertainty due to the lack of our capability to predict the respective and interactive effects.

The primary effect of elevated CO_2 concentration ([CO_2]) on crop productivity is enhancement of photosynthesis, which has been well studied for many years. The resultant effects on crop growth and susceptibility to biotic and abiotic stresses have not been studied in enough detail to predict the magnitude and even the direction of these effects. Experiments are needed to reduce uncertainties in factors that are involved in future crop productivity prediction,

The changes in climates can affect not only crop growth and development but also materials cycling and energy flow in agricultural ecosystems. These changes can in turn influence crop productivity. These secondary or indirect effects have been at the level of qualitative conjecture and not have been taken into consideration in the predictions of global change impacts due to lack of experimental evidence. These interactive effects of climate change on agro-ecosystems may be handled by process-based models that include major processes in the agro-ecosystems, but models developed so far cover only limited aspects of the effects.

2. Research Objectives
This research project has two major objectives:
(1) to determine the effects of increasing [CO_2] and temperature on crop growth and susceptibility to biotic and abiotic stresses such as diseases, insects and extreme temperature events.

For this purpose, we conducted FACE (free-air CO_2 enrichment) experiments in Shizukuishi, Iwate Prefecture and TGC (temperature-gradient chambers) experiments at the National Agricultural Research Center for Tohoku Region, Morioka, Iwate Prefecture. Under this objective, we conducted research on the following specific subjects:

A. Improvement of the FACE system in farmer's field,
B. Biomass and yield responses to elevated [CO_2] under field conditions and their differences among genotypes and N treatments,
C. Elevated [CO_2] effects on heat and chilling induced spikelet sterility and occurrence of immature grain under high temperatures,
D. Phenology response to elevated [CO_2] its genotypic variation,
E. Elevated [CO_2] effects on susceptibility to rice to blast and sheath blight diseases, and
F. Life history traits of winged (alate) and wingless (apterous) viviparous foxglove aphids (*Aulacorthum solani* Kaltenbach) that mediate soybean dwarf virus as affected by food plant growth conditions.

(2) Improvement of the process-base model and its testing

For this purpose, we tested whether DNDC, a biogeochemical model of various ecosystems developed by C. Li of New Hampshire University [1)], can reproduce the effects of elevated [CO_2] on crop growth and metabolisms of carbon and nitrogen in the FACE experiments. By identifying problems with the current version of the model, we have made necessary modifications to the model in crop growth and soil processes.

3. Research Methods and Results

(1) Impacts of increasing [CO_2] and temperature on crop growth and susceptibility to diseases and insects

A. Improvement of the FACE system

The FACE system developed and installed in the first-phase FACE in Shizukuishi (1998-2000) injected pure CO_2 gas from three windward tubes out of the eight plastic tubes that form an octagonal shape of the plot[2)]. We developed a new system that controls pressure of each tube independently depending on the wind direction. The new system reduced CO_2 consumption by 20 % at no expense of accuracy.

B. Biomass and yield responses to elevated [CO_2] and their differences among genotypes and N treatments

Five rice cultivars of different maturity (Kirara 397, Kakehashi, Akitakomachi, Hitomebore and Koshihikari) were grown in paddy fields under two [CO_2] conditions. Earlier varieties generally showed larger enhancements of biomass and yield enhancements by elevated [CO_2] than later varieties. Differences in biomass enhancement by elevated [CO_2] amongst cultivars, N treatments and years, could well be related with plant nitrogen concentration at the panicle initiation stage: Low N concentration at the panicle initiation stage resulted in low biomass and yield enhancements by elevated [CO_2] at harvest. Noticeable lodging occurred under the high N treatment, but the FACE treatment significantly reduced the degree of lodging.

C. Elevated [CO_2] effects on heat and chilling induced spikelet sterility and occurrence of immature grain under high temperatures

Rice cultivar 'Sasanishiki' grown in pots under two TGC's of different [CO_2] conditions was treated with cool water of 19.5 ^{o}C during the reproductive period for three growing seasons. Percentage of sterile spikelets caused by the cool water treatment increased significantly with increased number of spikelets. This suggests that the positive effect of elevated [CO_2] on spikelet number reported previously[3)] can partially offset by the cool summer damage.

2003 was a year of cool summer, and an early cultivar 'Kirara 397' provided for the FACE experiment was exposed to cool air at the critical stage for reproductive development. Increased spikelet density by the FACE treatment decreased percentage of fertile spikelets, confirming for the first time that the cool damage on spikelet fertility is exacerbated by elevated [CO_2] under a field condition; a finding of significant agronomic importance.

Heat induced spikelet sterility (HISS) is the major concern under warmer environments in the future. Only a few hours of heat around flowering time can reduce spikelet fertility substantially. Elevated [CO_2] has been reported to exacerbate HISS, but the reasons remain unclear. One possible mechanism by which elevated [CO_2] exacerbates HISS is that elevated [CO_2] increases canopy and panicle temperatures due to reduced transpiration[4)]. Another possibility is that accumulated effects of elevated [CO_2], which may change the susceptibility to HISS; this has not been tested experimentally, nor has any direct effect of [CO_2]. To determine the direct effects of elevated [CO_2] and indirect effects through pre-flowering [CO_2] conditions, we developed a panicle chamber to accurately control temperature and humidity around panicles. We did not observe neither significant effects of pre-flowering [CO_2] conditions nor direct effects of elevated [CO_2].

An emerging problem for Japanese rice industry is degraded grain quality due to white (usually opaque) grains. Incomplete grain filling caused by high temperatures during the early ripening period are the major reasons for this, but the effect of elevated [CO_2] has not been determined experimentally. We therefore grew rice plants (cv 'Koshihikari') in a mini-chamber at the warmest part of TGC at day/night temperatures of 35/28 ^{o}C for two weeks after flowering. The heat treatment increased % of immature grain substantially compared to control, but no significant impact of elevated [CO_2] was detected. These results indicate that the effect of elevated [CO_2] on HISS and grain filling likely appear through increased canopy and spikelet temperatures.

D. Phenology response to elevated [CO_2] its genotypic variation

Warmer climates accelerate crop development but previous studies indicated that elevated [CO_2] also hastens the occurrence of phenological events. Three-year variety trials in TGC have shown that the effect of elevated [CO_2] on the heading time is different amongst genotypes and years: Advancement of heading due to elevated [CO_2] was noted in medium-maturity varieties from Tohoku district, but only limited response was observed for early varieties from Hokkaido. The effect was not marked under poor solar radiation conditions. We tested whether any interactive effect of elevated [CO_2] and temperature on phenology using an experimental system in the TGC, by which water temperature (i.e. below-ground and meristem temperatures) and air temperature could be controlled independently. Interestingly, advancement of panicle initiateon due to elevated [CO_2] was marked only under low air temperature. This suggests that the genotypic variation in phenology response to elevated [CO_2] could be ascribed to thermal sensitivity of the aerial parts of the plant, not the meristem.

E. Elevated [CO_2] effects on susceptibility to rice to blast and sheath blight diseases

Rice plants grown in the FACE experiments were inoculated with blast fungus. We observed higher incidence of blast disease under FACE than under control, which was consistent with the previous observations in the FACE and TGC experiments[5)]. The FACE treatment significantly reduced silicon content of leaf blades that could possibly reduce the resistance to the penetration of the fungus.

The FACE treatment also increased incidence of rice sheath blight both under natural and inoculated conditions. This was because the FACE treatment accelerated the spread of sheath blight from one hill to another. The larger number of tillers in the FACE treatment might have made hill-to-hill contacts more frequent or canopy microclimate more favorable for the fungi.

F. Life history traits of winged and wingless viviparous foxglove aphids

Winged and wingless viviparous Foxgolve aphids (*Aulacorthum solani* Kaltenbach) were fed with soybean leaves grown under elevated and ambient [CO_2] in TGC and their life history traits were measured. Feeding soybean leaves from plants grown under elevated [CO_2] conditions significantly influenced some life history traits, but no positive effects of elevated [CO_2] were detected on the intrinsic rate of natural increase winged and wingless viviparous foxglove aphids. It is therefore not likely that the foxglove aphids will increase with increasing [CO_2] to aggravate soybean dwarf virus disease.

(2) Modification of the plant and soil processes model and its testing

We tested MACROS (Modules of an Annual CROp Simulator) [6)], a model that was developed to express carbon metabolism of the plant, against the measurements in the FACE experiments in Shizukuishi. The model overestimated the effect of elevated [CO_2] but underestimated the effect of N application. In the model, an empirical multiplier was used to represent the photosynthetic enhancement by elevated [CO_2]: This is one of the reasons for overestimation of the [CO_2] effect. Leaf area was calculated as a function of biomass increase so that the biomass enhancement due to elevated [CO_2] directly reflected the leaf area enhancement in the model: This resulted in a feed-forward enhancement of elevated [CO_2]. However, observed leaf area was not stimulated by elevated [CO_2] as much as it was predicted: This is another source of error in estimating plant responses to [CO_2] and N.

To account for CO_2 effects on photosynthesis explicitly on the basis of biochemical responses, we introduced Farquhar's photosynthesis model[7)], which, in principle, assumes that the photosynthetic rate is limited either by carboxylation or RuBP (Riblose 1,5-bisphosphate) regeneration in the Calvin Cycle. Two major parameters in Farquhar's model were measured under different [CO_2] conditions under field (FACE) and chamber conditions (based on the in situ gas exchange measurements). Both maximum carboxylation rate (Vc,max) and maximum electron transport rate (Jmax) were highly and positively correlated with leaf N content: This relationship can be used as a robuts basis for photosynthesis estimation. Canopy photosynthesis was estimated by integrating leaf photosynthesis derived from Farquhar's model with respect to leaf area, which was compared with measured photosynthesis of rice canopy grown in the closed chambers under ambient and ambient +300 ppmv [CO_2] conditions (Sakai, unpublished data). Estimated photosynthesis agreed well with the measured; this proved ability of the model to simulate photosynthesis under different [CO_2] at the canopy level.

To improve leaf area estimation, a leaf area module proposed by Hasegawa and Horie[8)] was incorporated in the model: In this module, leaf area was estimated based on the crop N uptake and temperature. The modified model slightly overestimated the [CO_2] effect particularly under high N, but generally reproduced well crop N, leaf area, biomass and grain yield measured under different N and CO_2 conditions in the three-year FACE experiments in Shizukuishi.

To determine the effects of elevated [CO_2] on soil chemical traits, we e monitored the soil redox potential and some soil chemical properties in the FACE experiment in 2004 and 2005 to test whether elevated [CO_2] has any influence on soil chemical properties. We observed a significant increase in Mg^{2+} and Ca^{2+} concentrations in the soil solution by the FACE treatment, but the soil redox potential was unaffected by elevated [CO_2].

We tested the original DNDC model against the measurements in the FACE experiments. The original model largely overestimated the CH_4 flux, while underestimated redox potential under flooded soil conditions. Because CH_4 release occurs at the final step of a series of reduction processes and iron plays an important role in the electron donor-acceptor relationship under submerged condition, we modeled the rate of Fe^{3+} reduction as a function of temperature based on the literature data for Japanese paddy rice[9)] and expressed the soil redox potential as a function of Fe^{2+}. This function adequately explained the change in redox potential in the FACE experiment, so could be introduced to DNDC. The improved DNDC combined with the plant process model to estimate the carbon supply from the roots to soil could simulate well the time-courses of methane flux observed in the FACE experiments in 2004.

4. Discussion

The results from the previous FACE experiments conducted from 1998-2000 showed that the increase in [CO_2] by 200 ppmv will raise rice grain yield by 5 – 15 %: the magnitude depends on the amount of nitrogen application[3)]. In this study, variation in grain yield enhancement due to elevated [CO_2] amongst varieties of different maturity was related with N nutrition around the panicle initiation stage, suggesting that N and [CO_2] interaction is also important for selecting adaptive varieties to increasing [CO_2].

MACROS has been used as a prototype of many crop growth models for its comprehensiveness of the carbon metabolism, but fails to represent the interactive effects of [CO_2] and N on crop growth and development, indicating models based on carbon limited growth contain some intrinsic errors in predicting rice productivity under future environments. We introduced Farquhar’s photosynthetic model, the two major parameters being expressed as a function of leaf N, and N driven leaf area dynamics. The model was able to reflect the interactive effects of [CO_2] and N, but biomass under high N and [CO_2] was overestimated, indicating that other limiting factors are also involved.

One of the negative influences with heavy N application is susceptibility to lodging. In this study, moderate lodging occurred under high N conditions in 2004, the degree of lodging was less under FACE than under ambient. This is rather surprising because the bending moment should have been higher in FACE due to heavier panicles. It should be noted, however, efforts that will reduce the risk of lodging (e.g. resistant varieties) will remain important for the future rice production, because panicles weights are expected to increase and a fair amount of N would be needed to take advantage of higher [CO_2].

Heavier N application generally increases susceptibility to blast. The present study has also shown that elevated [CO_2] exacerbates blast and sheath blight diseases. Significantly lower silicon content of leaves under elevated [CO_2] than under ambient is a possible reason for increased blast disease susceptibility, while more frequent contacts between neighboring hills for faster sheath blight spread. These results suggest that combination of high [CO_2] and N application will likely increase the risk of major rice diseases, so that countermeasures against them need be strengthened: They may include silica application and/or planting pattern in combination with pest management practices.

Spikelet sterility caused by extreme temperatures is the largest source of yield fluctuation in Japan. The present study has, for the first time, provided evidence that elevated [CO_2] will increase susceptibility to chilling induced spikelet sterility. In the meantime, elevated [CO_2] is reported to exacerbate heat induced spikelet sterility. These results suggest that a temperature window for secure spikelet fertilization will be narrowed by elevated [CO_2]. The present study has also shown that these [CO_2] effects on spikelet sterility are largely through indirect effects, but quantitative understandings are very limited. Further studies on environmental responses of reproductive physiology in combination with heat budget of the canopy will be needed to improve prediction of [CO_2] and temperature interaction on spikelet sterility.

While global warming is projected to shorten growth duration, elevated [CO_2] further accelerates development. The present study revealed, however, that the effect of [CO_2] on phenology is different among genotypes. Genotypic variation in the phenology response to elevated [CO_2] may in turn affect biomass and yield enhancement via the effects on growth duration and accelerated senescence. Interestingly, advancement of panicle initiation due to elevated [CO_2] was marked only under low air temperature (i.e. temperatures around aerial parts). This suggests that the genotypic variation in phenology response to elevated [CO_2] could be ascribed to thermal sensitivity of the aerial parts of the plant, not the meristem. This finding may help improve our quantitative understandings of phenology.

Morphological traits of genotypes are also important for adaptability to elevated [CO_2]. As was shown in the present study, enhancement of grain yield is associated with tiller, panicle and spikelet numbers responses to elevated [CO_2]. On the other hand, methane flux from the paddy soil is increased by increased tillers and roots. The improved DNDC model along with a crop growth module can now account for both positive effects of morphological traits on crop productivity and negative ones on the emission of methane, a greenhouse gas with strong global warming potential, so can be used to evaluate adaptive options of rice cultivation in terms of both productivity and environmental impacts.

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