

Elevated temperature has stronger effects on the soil food web of a flooded paddy than does CO₂



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ABSTRACT

Paddy fields are valuable wetlands for both food production and conserving biodiversity. However, while global warming poses a major threat to biodiversity, evaluations on its impacts within flooded paddy fields have been very limited. Soil nematodes present an ideal model organism for this issue because they are dominant and diverse native animals within this system; moreover, they support aboveground biodiversity by serving as a food source for larger animals, and they are influential rice pests that affect our food output from paddy fields. We examined the effects of a predicted elevation in CO₂ and temperature over the next 50 years on the dynamics of dominant nematode taxa and their food source, i.e., rice roots and microbes in a flooded paddy field equipped with a FACE + heater system. We hypothesized that, 1) the impact of an elevation in CO₂ concentration (+200 ppm) would be dependent on the trophic level of the organisms (it would be greater on rice roots compared to microbes or nematodes), although the impact can be consistently detected on each of rice roots, microbes and nematodes, 2) the impact of an elevation in temperature (+2 °C) could affect each organism simultaneously but would be different among organisms due to possible differences in thermal optima. Within our 2-year study, only our temperature hypothesis was supported, i.e., that an elevation in temperature increased rice root biomass, if any, but consistently decreased microbial biomass and retarded reproduction in the nematode taxa, which are potential rice pests. Elevated CO₂ increased rice root biomass, but did not consistently affect microbial biomass or reproduction of any type of nematode taxon. We infer that the small and inconsistent impact of elevated CO₂ on both microbes and nematodes could be attributable to an insensitive growth response to an elevation in CO₂ concentration by the rice variety we examined.

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1. Introduction

Paddy fields are valuable wetlands for both food production and conserving biodiversity (Ramsar Convention Meeting, 2008). The tenth meeting of the Conference of the Parties to the Convention on Biological Diversity (2010) demonstrated that global warming is a major threat to biodiversity. Evaluations on the impact of global warming on flooded paddy ecosystems, however, have focused mainly on rice growth (e.g., Hasegawa et al., 2013) and biogeochemical activities such as methane emission (e.g., Tokida et al., 2013). Very limited information is available on the impact of future warming on wild animals and plants in flooded paddy ecosystems. Yamazaki et al. (2005) reported the dynamics of

planktonic animals and plants of paddy fields under elevated CO₂. However, they did not examine the impact of elevated temperature, the main and most direct influence of global warming, on these dynamics. They were also only able to study this system for a single year, which means that the repeatability of their results was not confirmed. In our present study, we evaluated the impacts of elevated CO₂ concentration and temperature both together on the soil food web of a paddy field, which supports aboveground biodiversity (Fernando et al., 2005). Among the soil biota, we focused on nematodes due to their taxonomical and functional diversity and their ability to be bioindicators of environmental disturbance and anthropogenic impacts (Bongers, 1990; Ferris et al., 2001; Neher, 2001; Okada and Harada, 2007). In terrestrial environments, many studies have been conducted to evaluate the possible impact of global warming on nematode communities as well as other forms of soil biota (Tylianakis et al., 2008; Blankinship et al., 2011; Li et al., 2013). Also in paddy fields, the impact of

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elevated CO₂ was measured on nematode communities (Bao et al., 2011). However, the study was made in a drained period after rice growth was over. No study has yet examined the impact of global warming on nematode dynamics in a flooded paddy field with growing rice despite their potential importance to soil food web functions.

In freshwater soil and sediment food webs, nematode functional groups include plant root-feeders, microbial-feeders, predators, or omnivores, and they play critical roles in various types of ecosystem functions. For example, *Hirschmanniella* spp. are plant root-feeders that can damage crop production, e.g., rice grain yield and root quality of edible lotus (Kawashima, 1992; Mihira, 2002; Bert and Borgonie, 2006). Oppositely, free-living benthic *Tobrilus* and *Aphelenchoides* spp. for example, are major food sources for young fish and other aquatic animals, and aid in supporting fishery productivity and wildlife conservation (Crisp and Lloyd, 1954; Schwank, 1981; Ajah et al., 2006). Within the soil of a Japanese paddy field, we found both of these nematode genera (e.g., Ishibashi et al., 1983; Okada et al., 2011), and when completing a preliminary survey, we determined that the abundances of enchytraeids and other soil animals were too small in our experimental plots to reliably evaluate the effect of elevated CO₂ concentration and temperature on these organisms.

To determine the response of nematodes to elevated CO₂ concentrations and temperature, we need to first examine the response of rice plants and soil microbes to these variables. Rice plants and soil microbes are potential food sources for nematodes and, therefore, may influence the response of nematodes to elevated CO₂ concentrations and temperature. A previous study examined the soil microbial response in a paddy field equipped with a free-air CO₂ enrichment (FACE) facility in northern Japan (annual mean temperature is 9.4 °C) and found that the microbial biomass carbon and nitrogen increased under elevated CO₂ during a flooded period (Hoque et al., 2001). Therefore we expected that in our paddy field, located in central Japan with a warm climate (annual mean temperature is 13.8 °C), rice plants and microbes would grow and reproduce faster than reported by Hoque et al. (2001) and that the effect of elevated CO₂ concentrations can also influence nematodes on the same trophic level as microbes or higher.

An elevation in temperature can directly affect the reproduction and survival of nematodes. The thermal optima for some species closely related to our target nematodes are known, e.g., 27–29 °C for reproduction of *Acrobeloides* spp. (bacterial-feeders) (Venette and Ferris, 1997). However, predicting the response of each nematode species or taxon to elevated temperature may be difficult because the thermal optima may differ within a single genus or taxa (Wallace, 1960; Younes, 1969; Huang et al., 1972; Rössner and Nagel, 1984).

Here, we hypothesize that the effect of elevated CO₂ concentration operates in a bottom-up manner in the soil food web, and that it has a larger impact on rice root biomass (primary producer) and a smaller but consistent impact on microbe and nematode biomass (primary or secondary consumers). We assume the microbes in our soil samples are mainly heterotrophs inhabiting below the soil surface, as we explain later. We also hypothesized that the effect of elevated temperature appears simultaneously on each trophic level, but differently among organisms, because their thermal optima may differ. To test our hypotheses we surveyed a paddy field in 2011 and 2012 that was equipped with a FACE + heating system in Tsukubamirai, central Japan. This machine simulates predicted CO₂ and temperature elevations expected in the year 2060 (i.e., ~50 years from now).

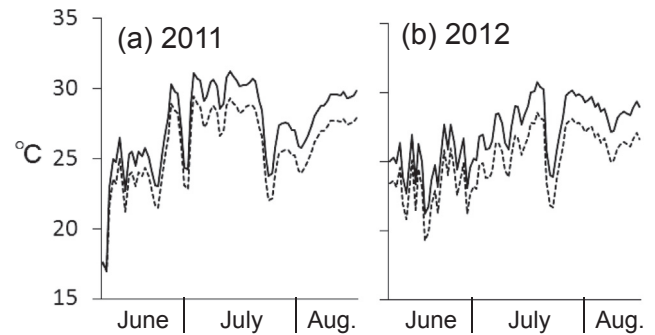


Fig. 1. Mean daily temperature from 1 June to 18 August in ambient plots at 37.5 mm soil depth, which was the exact center of 25–50 mm, the examined depth in our study in 2011 (a) and 2012 (b). Values are means across four replicate plots, which were calculated with temperatures at 0 and 100 mm depth, assuming a linear gradient between the two depths. Solid and broken lines indicate the elevated temperature (ET) and normal temperature (NT) subplots, respectively. Temperatures in free-air CO₂ enrichment (FACE) plots are not shown because their values were almost the same (only 0–0.3 °C difference) as those of corresponding ambient plots on a given day.

2. Materials and methods

2.1. Site and system description and cultivation management

Details of the study site, cultivation, soil physicochemical properties, and the FACE system have been described elsewhere (Hayashi et al., 2011; Nakamura et al., 2012; Hasegawa et al., 2013). Briefly, we installed the rice–FACE system in farmers' rice paddies in Tsukubamirai, Ibaraki, Japan (35°58'27"N, 139°59'32"E, 10 m above sea level). The chemical properties of the irrigated water in the experimental plots (means measured on 4 July 2011) were the following: DO, 12.0 mg/L; EC, 21.9 mS/m; and pH, 7.60.

We used four rectangular bays within each of the fields. The longer side of each bay was 100 m and the shorter one ranged from 30 to 70 m. Within each bay, we established an elevated CO₂ plot (hereafter referred to as "FACE") paired with a companion ambient plot. A pairwise comparison of the treatment in each bay ensured similar water management practices and homogenous soil properties in both the ambient and FACE plots. We separated the ambient and FACE rings (17 m diameter) by at least 70 m (center to center). We exposed the ambient plots to ambient CO₂ concentrations (379 and 383 ppm, mean from June to September 2011 and 2012, respectively). Our target degree of CO₂ elevation in FACE plots was 200 ppm above the ambient levels (actually 560 and 577 ppm, mean from June to September 2011 and 2012, respectively).

We conducted a single cropping of paddy rice (*Oryza sativa*) at each field in the conventional style of this region. We irrigated the paddy fields in late April and submerged them in early May in 2011 and 2012. We applied chemical fertilizers on 9 April 2011 and 2012 (P₂O₅ and K₂O, each 100 kg/ha) and again on 19 May 2011 and on 14 May 2012 (N, 80 kg/ha), and we incorporated with puddling as the basal fertilization. We transplanted rice seedlings (three seedlings per hill) of a japonica variety ("Koshihikari") on 23–24 May 2011 and 2012 with a density of 22.2 hill m⁻² (spacing of 0.3 m × 0.15 m). We chose this variety because it is the most popular in Japan (nearly 40% of all the varieties cultivated). We set up subplots (3 × 3.6 m) for temperature treatments to accommodate 10 rows of rice plants in each FACE and ambient plot in late May. We tried to keep the temperature 2 °C higher in elevated temperature (ET) plots than in normal temperature (NT) plots until the end of the flooded period (late August) by submerging line heaters and thermo-sensors along rice plant rows in ET. Mean temperatures at the mean depth of soil samples examined (37.5 mm) from 1 June to 18 August (just before

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