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Physiology of yield determination of rice under elevated carbon dioxide at high temperatures in a subhumid tropical climate

W.A.J.M. De Costa [a,*], W.M.W. Weerakoon [b], H.M.L.K. Herath [c], K.S.P. Amaratunga [d], R.M.I. Abeywardena [a]

[a] Department of Crop Science, Faculty of Agriculture, University of Peradeniya, Peradeniya 20400, Sri Lanka
[b] Rice Research and Development Institute, Batalagoda, Ibbagamuwa, Sri Lanka
[c] Rubber Research Institute, Agalawatta, Sri Lanka
[d] Department of Agricultural Engineering, Faculty of Agriculture, University of Peradeniya, Peradeniya 20400, Sri Lanka

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Abstract

A substantial portion of rice in South Asia is grown in tropical and sub-tropical climates under relatively high temperatures (i.e. >30 °C). Increases in atmospheric carbon dioxide (C_a) concentration have been shown to increase total biomass and grain yield of C_3 crops including rice. However, doubts have been expressed whether the expected yield increases in response to increased C_a could be sustained under high temperature regimes. Therefore, the main objective of the present study was to quantify the response of rice to elevated C_a at high temperatures (i.e. >30 °C) in a sub-humid tropical environment in terms of radiation interception, radiation use efficiency (RUE) and biomass partitioning to grains. It was also investigated whether RUE of rice growing under elevated C_a decreases during the post-heading period, possibly due to a reduction of leaf nitrogen concentration.

Rice was grown over two seasons in a sub-humid tropical climate in Sri Lanka at elevated (ca. 567 ± 28 μmol mol^{-1}) and ambient (ca. 363 ± 16 μmol mol^{-1}) C_a in open top chambers with open field plots to estimate chamber effects. C_a within chambers was maintained around target concentrations by a computer-based real time data acquisition and control system. Radiation interception was measured continuously by tube solarimeters. Seasonal fraction of incoming radiation intercepted did not change with CO_2 enrichment. Rice under elevated C_a showed significantly greater (20% and 11% in the two seasons) RUE relative to ambient C_a. RUE under elevated C_a did not show a reduction during the post-heading period. Consequently, the total biomass at harvest was 23–37% greater under elevated C_a. Number of grains initiated and percentage of grains filled were significantly greater under elevated C_a resulting in final seed yields being 24% and 39% greater than the ambient. During grain filling, the fraction of biomass partitioned to grains under elevated C_a did not exceed that under ambient C_a. Based on the above results, it is concluded that rice yields respond positively to increasing C_a even at the higher range of growing temperatures. Greater RUE and greater initiation of grains are the primary causes of this yield stimulation at the crop level.

Keywords: *Oryza sativa* (rice); Elevated CO_2; High temperature; Radiation use efficiency; Biomass partitioning; Grain filling; Open-top chambers

1. Introduction

Atmospheric carbon dioxide concentration (C_a) has been increasing exponentially during the last 250 years (Goudriann, 1995; Prentice, 2001; Houghton et al., 2001; Keeling and Whorf, 2002). According to the different CO_2 emissions scenarios formulated by the Intergovernmental Panel on Climate Change (IPCC), the respective ranges for C_a by 2050 and 2100 are 463–623 and 478–1099 ppm (McCarthy et al., 2001). Most of the realistic policy initiatives aim to stabilize C_a at 550 or 650–700 ppm levels by 2050 and 2100, respectively.

Rising C_a can be sensed by plant tissues, which are directly in contact with the atmosphere. Long et al. (2004) have shown that elevated C_a increases the C_3 photosynthetic rate at the cellular level through increased carboxylation and decreased oxygenation, both of which are catalyzed by

* Corresponding author. Tel.: +94 81 2388239; fax: +94 81 2388041.
E-mail address: janendrad@yahoo.com (W.A.J.M. De Costa).

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Rubisco. Several reviews have shown that the above increase in photosynthetic rates is translated to increases in biomass production and yield of agricultural crops (Kimball, 1983; Cure and Acock, 1986; Lawlor and Mitchell, 1991; Jablonski et al., 2002) and natural plant species (Norby et al., 1999; Poorter and Navas, 2003).

Rice is the staple food of most of the South Asian countries including Sri Lanka. Therefore, it is important to determine how rice yields are influenced by elevated C_a as it would have crucial implications on future food security of this highly-populated region of the world. Most of the CO_2 enrichment experiments conducted during the last decade have shown that rice yields increase in response to elevated C_a (Baker et al., 1990, 1996; Ziska and Teramura, 1995; Ziska et al., 1997; Moya et al., 1998; Kim et al., 2001, 2003). The observed yield increases showed a wide variation (i.e. 5–60%), which may be due to a variety of reasons such as the genotype and interactions between elevated C_a and other environmental factors. Research data on the response of rice to elevated C_a at high temperatures (i.e. >30 °C) in humid tropical environments, which represent a large portion of rice-growing regions in South Asia, is sparse. Therefore, the main objective of the present study was to determine the yield response of rice to elevated C_a at high temperatures and elucidate its physiological basis at the crop level.

Physiological basis of yield variation of a crop can be analyzed in terms of the following equation,

$$Y = S \times F \times \mathrm{RUE} \times \mathrm{HI} \quad (1)$$

where Y is the grain yield, S the total incident solar radiation over the entire duration of the crop, F the fraction of incident radiation intercepted by the crop, RUE the radiation use efficiency (i.e. biomass produced per unit of radiation intercepted) and HI the harvest index. Therefore, at least one or more of the components of Eq. (1) has to increase for rice yield to increase under increased C_a. F depends on the leaf area index (LAI) of the crop and its canopy architecture (Monteith, 1981). Some of the previous workers have observed both increases (Kim et al., 2001) and decreases (Ziska and Teramura, 1995) of LAI of rice under elevated C_a, while an extensive review by Drake et al. (1997) found that LAI did not change significantly. On the other hand, there is no information about the influence of increased C_a on canopy architecture.

Both Drake et al. (1997) and Long et al. (2004) have shown that C_3 light use efficiency at the cellular level is increased with increased carboxylation efficiency under elevated C_a. However, only a few studies have verified this in the field at the crop level over a growing season. In the only previous work on radiation use efficiency (RUE) of rice under elevated C_a, Weerakoon et al. (2000) observed a 35% increase in RUE at higher C_a as compared to that at ambient C_a. However, Weerakoon et al. (2000) also observed a reduction of RUE with crop age under elevated C_a, which was attributed to a reduction in specific leaf nitrogen concentration. These aspects of radiation interception and conversion will be examined in the present study.

While many previous workers have investigated the processes leading to biomass production of rice under elevated C_a, few have examined biomass partitioning into grains. Imai et al. (1985) and Allen et al. (1995) have reported increases in harvest index (HI) under elevated C_a, whereas Baker et al. (1992), Ziska et al. (1997) and Kim et al. (2001) have observed decreases. HI is determined by the number of grains initiated and the rate of growth of those grains. Biomass for grain growth of rice can come from both current photosynthesis and re-translocation from vegetative parts (Yoshida, 1981). If the photosynthetic capacity of the canopy decreases during the grain-filling period due to a reduction of specific leaf N (Weerakoon et al., 2000), assimilate re-translocation to grains is likely to increase. These aspects will also be investigated in the present paper.

2. Materials and methods

2.1. Description of experimental site

Two field experiments were carried out in a lowland paddy at the Rice Research and Development Institute, Batalagoda of Sri Lanka ((7°50′N, 80°50′E) during 2001. The two growing seasons were from January to March (i.e. *maha* season) and from May to August (i.e. *yala* season). The site is located within the sub-humid zone known as the Low-country Intermediate Zone (Panabokke, 1996). It has a bi-modal rainfall pattern with the annual total ranging from 1500 to 2285 mm. A high proportion of this total is received during the *maha* season. The daily mean temperature ranges from 28 to 32 °C. The soil type was Low-Humic Gley (Order—Alfisols; Sub-order—Aqualfs; Great group—Tropaqualfs) with a pH of 5.9 and electrical conductivity (EC) of 0.7×10^{-4}.

2.2. Experimental treatments

There were three experimental treatments replicated twice in a randomized complete block design. The 'elevated C_a' treatment had rice growing in open top chambers (OTCs) enriched with a mixture of pure CO_2 and air to a mean target concentration of 570 μmol mol^{-1} from sowing until harvesting. In the 'ambient C_a' treatment, rice was grown in OTCs without CO_2 enrichment under the ambient CO_2 (i.e. around a mean of 370 μmol mol^{-1}) concentration. In the 'open' treatment, rice grown in open plots under normal atmospheric conditions. This treatment was used to detect any effects that the presence of the chamber would have had on crops.

2.3. Design and construction of open top chambers

The OTCs were made with an aluminium frame covered with UV-treated polythene. The frame was approximately