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Plasticity of rice tiller production is related to genotypic variation in the biomass response to elevated atmospheric CO_2 concentration and low temperatures during vegetative growth

Hiroyuki Shimono*, Masumi Okada

National Agricultural Research Center for Tohoku Region, Shimokuriyagawa, Iwate 020-0198, Japan

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ABSTRACT

Appropriate resource partitioning to either production of new tillers or growth of individual tillers is a critical factor for increasing rice biomass production and facilitating adaptation to climate change. We examined the contributions of genotypic variation to the tiller number and individual tiller growth of 24 rice cultivars in response to an elevated atmospheric CO_2 concentration [CO_2] (control + 191 μmol mol^{-1}) and a low air temperature (control minus 4.7 °C) during 56 days of vegetative growth after transplanting. For all genotypes combined, biomass increased by 27% under elevated [CO_2] and decreased by 34% at low temperature, with a significant genotype × temperature interaction. The increase caused by elevated [CO_2] resulted from increased tiller number, and the decrease caused by low temperature resulted from decreased growth of individual tillers. Despite the different overall responses to elevated [CO_2] and low temperature, most of the genotypic variation in biomass at elevated [CO_2] and low temperature was explained by the responses of tiller number rather than by individual tiller growth. The genotypes with the highest biomass response to elevated [CO_2] had a smaller reduction of biomass under low temperature. These results highlight the greater importance of genotypic variation in tiller number than in individual tiller growth in the response of biomass to environmental change.

1. Introduction

Rice (*Oryza sativa* L.), one of the world's most important cereals, has been adapted by breeders to a wide range of environments ranging from 35°S to 53°N in latitude and from 0 m to more than 2000 m in altitude (Yoshida, 1981). As a result of this adaptation, rice is grown in a wide range of ecosystems around the world. Its flexibility in tiller production is one of its most important traits for adaptation to its environment. An increase in tiller number can increase canopy photosynthesis by increasing the area of green leaves and the associated transpiration, and can increase the panicle number, which determines grain number and weight (Baker, 2004; Boonjung and Fukai, 1996; De Costa et al., 2007; Ishii et al., 2011; Luquet et al., 2005; Moya et al., 1998; Peng et al., 2000; Shimono, 2011; Takai et al., 2006; Takeda et al., 1984; Ziska et al., 1996).

It is well known that there is synchronism between leaf and tiller emergence, with a systematic rule for initiating new tillers based on leaf appearance on the main stem and on the tillers; specifically, rice is constituted from phytomers, with one per phyllochron stage and with the stage defined by the appearance of new leaves at consistent time intervals (Nemoto et al., 1995). A rice plant at the 13th phyllochron potentially has more than 100 tillers (Goto and Hoshikawa, 1988). However, under normal environmental conditions in the field, the tiller number never reaches this potential. Similarly, the growth of individual tillers, and the associated increases in the weight of leaves, leaf sheaths, culms, and panicles, also has limits, since this growth is constrained by limitations on the supply of carbohydrates, water, and nutrients. Appropriate and efficient resource partitioning to either the production of new tillers or the growth of individual tillers would increase a genotype's biomass production under a given set of environmental conditions.

Researchers who compared old and modern genotypes have reported high genotypic variation in the biomass partitioning pattern, and specifically in whether a genotype tends to produce more new tillers or increase the growth of individual tillers (Anzoua et al., 2010; Peng et al., 2000; Takeda et al., 1984). The older genotypes tend to have fewer tillers and heavier panicles than modern genotypes, but there are also differences among the subspecies of rice (i.e., *indica*, *japonica*, *javanica*; Takai et al., 2006).

Both the production of new tillers and the growth of individual tillers by any genotype may decrease under resource constraints or environmental stress, or may improve when these constraints

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* Corresponding author. Present address: Crop Science Laboratory, Faculty of Agriculture, Iwate University, 3-18-8, Ueda, Morioka, Iwate 020-8850, Japan. Tel.: +81 19 621 6146; fax: +81 19 621 6146.

E-mail address: shimn@iwate-u.ac.jp (H. Shimono).

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Table 1
Total dry weights of 24 rice genotypes in the control, low temperature, and elevated atmospheric CO_2 treatments.

No	Genotype	Origin	Total dry weight (g per plant)							
			Control		Low temperature			Elevated [CO_2]		
1	Kirara 397	Japan, Modern	9.7	±0.4	7.3	±0.9	(0.76)	14.1	±1.9	(1.45)
2	Kakehashi	Japan, Modern	9.5	±0.9	7.8	±1.6	(0.83)	11.6	±3.2	(1.23)
3	Akitakomachi	Japan, Modern	7.8	±1.9	5.5	±0.8	(0.70)	8.1	±0.9	(1.04)
4	Hitomebore	Japan, Modern	6.6	±0.4	4.9	±0.7	(0.74)	8.6	±1.0	(1.30)
5	Koshihikari	Japan, Modern	8.2	±0.4	6.6	±1.3	(0.81)	10.9	±2.1	(1.33)
6	Norin 8	Japan, Old	12.4	±2.6	6.0	±0.6	(0.49)	11.1	±1.0	(0.89)
7	Morita-wase	Japan, Old	12.4	±1.1	7.8	±0.5	(0.63)	16.8	±0.5	(1.36)
8	Kameno-o 4	Japan, Old	13.2	±0.9	9.3	±0.3	(0.70)	15.1	±2.0	(1.14)
9	Rikuu 132	Japan, Old	11.1	±1.2	6.4	±0.3	(0.57)	14.0	±1.4	(1.26)
10	Bekoaoba	Japan, High yield	9.0	±1.1	7.4	±0.6	(0.82)	11.9	±1.5	(1.32)
11	Takanari	Japan, High yield	7.5	±2.0	5.0	±0.5	(0.67)	8.3	±1.1	(1.11)
12	Lemont	U.S.A.	7.5	±1.8	4.6	±0.7	(0.61)	9.0	±0.4	(1.20)
13	Darumari	Nepal	25.9	±1.0	15.7	±1.4	(0.61)	33.6	±0.8	(1.30)
14	Pakhe Dhan	Nepal	14.5	±0.9	10.0	±1.2	(0.69)	20.0	±0.7	(1.38)
15	Koukoutouji	China	11.2	±0.8	6.4	±1.0	(0.57)	14.4	±1.5	(1.28)
16	Xingingai	China	10.2	±3.1	6.3	±0.8	(0.62)	12.4	±3.2	(1.22)
17	Tyuugoku 99-15	China	3.9	±0.3	3.2	±0.1	(0.82)	5.6	±0.3	(1.41)
18	Calrose	U.S.A.	8.1	±1.0	5.8	±0.6	(0.71)	12.9	±0.9	(1.58)
19	Italica Livorno	U.S.A.	17.8	±1.3	11.4	±0.3	(0.64)	21.7	±1.0	(1.22)
20	Arroz da Terra	Portugal	15.2	±1.4	9.4	±0.8	(0.62)	21.7	±2.6	(1.43)
21	Amaroo	Australia	7.9	±0.2	5.5	±0.8	(0.70)	11.5	±1.6	(1.46)
22	RP 9-3	India	6.2	±0.7	6.7	±1.0	(1.09)	13.8	±2.2	(2.21)
23	BG 34-8	Sri Lanka	11.3	±0.9	8.1	±1.0	(0.72)	10.8	±0.1	(0.96)
24	Taichungsen 10	Taiwan	8.6	±1.2	6.2	±0.4	(0.72)	9.5	±1.3	(1.10)
	Maximum		26		16		(1.09)		34	(2.21)
	Minimum		4		3		(0.49)		6	(0.89)
	Average		11		7		(0.70)		14	(1.30)
	CV (%)		42		36		(17.0)		43	(19.6)
	ANOVA	Treatment (A)				**				
		Cultivar (B)				**				
		A × B				**				

Values are the means of three replicates ± standard errors (with the ratio of the treatment value to the control value in parentheses). $^{**}P < 0.01$.

decrease. There are reports of genotype–environment interactions in response to changes in a single environmental condition, such as atmospheric CO_2 concentration ([CO_2]; Baker, 2004; Shimono et al., 2009), drought (Ding et al., 2011), temperature (Andaya and Mackill, 2003; Baker, 2004), salinity (Asch and Wopereis, 2001), light (Nakano et al., 2008), and soil fertility (Saito and Futakuchi, 2009). There are also reports of responses to simultaneous changes in two or more environmental conditions, such as [CO_2] and temperature (De Costa et al., 2007; Moya et al., 1998; Ziska et al., 1996). However, most of these studies focused on the final grain yield, and changes in tiller behavior were expressed only in terms of the panicle number at maturity, which results from complicated and often indirect interactions such as changes in the sink–source balance (e.g., Shimono et al., 2010). However, understanding of the role of genotypic plasticity in resource partitioning between the creation of new tillers and the growth of existing individual tillers is important for future breeding. This is particularly important in the context of predicted future climate change, which is likely to have significant effects on biomass growth.

Tillering behavior varies greatly among cultivars (Anzoua et al., 2010; Peng et al., 2000; Takai et al., 2006; Takeda et al., 1984): some cultivars have high tillering capacity and others have not. Here, we hypothesized that rice genotypes with high tillering capacity would have a high potential for altering their allocation to tillering and thereby exhibiting high plasticity in response to environmental changes, which will help plants with these genotypes to adapt to a changing climate. Although the most commonly predicted effect of climate change will be global warming caused by elevated [CO_2], this warming will also permit earlier planting, and this means that rice may be exposed to colder temperatures during crucial parts of the vegetative growth period. To examine the ability of rice to respond to changes in [CO_2] and temperature, we exposed 24 rice cultivars with different origins to two environments: one represented enriched conditions, with elevated [CO_2], and the other represented a resource shortage, with a low temperature.

2. Materials and methods

We conducted a pot experiment in sunlit temperature-gradient chambers (Okada et al., 2000) in which [CO_2] and temperature conditions were controlled independently. The study was conducted at the National Agricultural Research Center for Tohoku Region, Japan (39°74′N, 141°13′E). Each chamber is a 6 m-wide by 30 m-long greenhouse. A temperature gradient is created along the long axis of the chamber by controlling three exhaust fans at the air outlet of the chamber, combined with the use of a pre-air-conditioning facility to cool incoming air at the air inlet of the chamber and with a heating system. CO_2 gas was introduced at the air inlet of the chamber and was controlled at approximately 200 ppm higher than the ambient [CO_2].

Seeds from 24 rice cultivars with a range of origins (Table 1) were sown in cell trays (one seed per cell) on 12 May 2005. [CO_2] was controlled at two levels (ambient and elevated, with the latter ca. 200 μmol mol^{-1} above ambient for 24 h a day). Each seedling was transplanted on 3 June 2005 into a pot containing 0.5 L of paddy soil (a typical gray lowland soil, equivalent to a Eutric Fluvisol). Plants were grown under one of three conditions: a control with the normal warm air temperature under ambient [CO_2]; a low-temperature treatment with air temperature about 5 °C lower than ambient, but with ambient [CO_2]; and an elevated [CO_2] treatment but with normal warm temperatures. All measurements were obtained during the vegetative growth period from transplanting to 56 days later (7 July). We used three replicates (i.e., $n = 3$ plants) for each cultivar. The air temperature during the treatment period in the control and elevated [CO_2] treatments averaged 22.8 ± 1.3 °C (mean ± standard deviation), whereas that in the low temperature