Responses of Eighteen Rice (*Oryza sativa* L.) Cultivars to Temperature Tested Using Two Types of Growth Chambers

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Abstract: Genetic variation in the growth response to temperature is a basis for developing adaptation measures to global warming, but evaluation of cultivars for the temperature responses may depend on other environmental factors such as light. In this study, we tested the growth responses of 18 diverse rice cultivars to constant day/night temperature of 25, 28, 31 and 34ºC in artificially-lit growth chambers (ALC) in Wagga Wagga (7.8 MJ m^{-2} d^{-1}), and in naturally-lit chambers (NLC) in Yanco (25 and 28ºC and 13.4 MJ m^{-2} d^{-1}; 31 and 34ºC and 11.5 MJ m^{-2} d^{-1}), both in NSW, Australia. There was a significant interaction between temperature and chamber type for total shoot and panicle biomass; total shoot biomass was largest at 31ºC in ALC, and at 25 and 28ºC in NLC. From the average of all temperatures, the total shoot biomass declined by 29.5% in plants grown in ALC compared with those grown in NLC. Importantly, cultivar performance in ALC was similar to that in NLC at these temperatures, as evidenced by the highly significant correlation in total shoot biomass between ALC and NLC. Among 18 cultivars, IR64, IR72, N22, Vandana, Takanari and Koshihikari commonly produced a larger total shoot biomass under higher temperature conditions. Leaf area at earlier measurement date was highly correlated with the final total shoot biomass at the higher temperature more than specific leaf area.

Key words: Artificially-lit chamber, High temperature, Naturally-lit chamber, *Oryza sativa* L., Panicle biomass, Rice, Total shoot biomass.

Global rice production needs to be increased by 40% by 2030 to support the growing global demand for this commodity (Khush, 2006). This increase has to occur under the anticipated higher global atmospheric temperatures of between 2.0 and 4.5ºC, which are predicted to occur by the end of the 21st century (IPCC, 2007). The use of existing high-temperature-tolerant rice cultivars or the development of high-temperature-adapted cultivars may minimize the deleterious effects of elevated temperatures and allow for increased global rice production to occur. The breeding of higher-temperature-tolerant or -adapted rice cultivars is the research aim of many agricultural researchers in order to meet increased production targets by 2030.

In its fourth assessment, the Intergovernmental Panel on Climate Change (IPCC) indicated that, over the next several decades, changes in global climate patterns should be experienced (IPCC, 2007). This report indicated that, for the land mass of tropical regions, where a considerable portion of the global rice crop is grown, mean annual temperatures are likely to increase, and would be accompanied by a probable increase in mainly wet-season rainfall; in contrast, in southern Australia, temperatures are expected to continue to increase, while rainfall is predicted to decline further (IPCC, 2007).

Solar radiation is another climatic parameter that will probably change over time, but it is erratic and past trends are inconsistent over time (Wild et al., 2005). Future predictions of solar radiation are uncertain, as solar radiation will be affected by changes in cloud patterns and in the suspension of particles in the atmosphere (Randall et al., 2007; Booth et al., 2012). Yet, solar radiation has a major influence on irrigated rice production (Yoshida, 1981). Spatial and temporal variation in solar radiation is

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Table 1. Cultivar name, germplasm group, level of heat tolerance and references of seed materials used during the experiment.

Cultivar name	Germplasm group	Level of heat tolerance[a]	References
1. Akihikari	*Japonica*	M	Matsui and Omasa, 2002
2. Akitakomachi	*Japonica*	T	Matsui and Omasa, 2002
3. Amaroo	*Japonica*	M	Matsui et al., 2007
4. Calrose	*Japonica*	VS	Yoshida et al., 1981
5. Cocodrie	*Tropical japonica*	S	Baker, 2004
6. Cypress	*Tropical japonica*	S	Baker, 2004
7. IR64	*Indica*	S-T	Jagadish et al., 2008
8. IR72	*Indica*	M	Prasad et al., 2006
9. Jefferson	*Tropical japonica*	S	Baker, 2004
10. Koshihikari	*Japonica*	M	Prasad et al., 2006; Matsui et al., 2005
11. Langi	*Japonica*	M	Matsui et al., 2007
12. Lemont	*Tropical japonica*	T	Jagadish et al., 2008
13. M103	*Japonica*	M	Prasad et al., 2006
14. N22	*Indica*	VT	Prasad et al., 2006; Jagadish et al., 2008
15. Nipponbare	*Japonica*	T	Matsui and Omasa, 2002; Matsui et al., 2005; Takai et al., 2006
16. Takanari	*Tongil*	VS	Matsui et al., 2005; Takai et al., 2006
17. Vandana	*Aus/japonica*	S	Jagadish et al., 2008
18. WAB 450-I-B-P- 38-HB	*Glaberrima/japonica*	VS	Matsui et al., 2005

[a]M = moderate; T = tolerant; VS = very susceptible; VT = very tolerant; S = susceptible.

one of the major factors that affect potential yields of rice (Evans 1993; Horie et al., 1997; Katsura et al., 2007). Projected rises in surface temperatures are likely to occur in areas with different light conditions. Adaptation of new cultivars to higher temperatures therefore needs to be tested under diverse light conditions. The phenotypic traits that may lead to stable performance under high temperatures under different growing conditions will be valuable in the search for source materials to breed new rice cultivars.

Because temperature and light conditions are important climatic factors, their combined effects on growth, yield and quality of rice have been major research targets (Matsushima, 1957; Murata, 1964; Yoshida and Parao, 1976). There is some evidence that the effects of temperature on rice grains could be mitigated by light conditions. Matsushima (1957) showed that, under shaded conditions, the negative effects of high temperature on seedling growth were more pronounced, while the effects of low temperatures were less severe under shaded than under non-shaded conditions. Some studies have attempted to determine the mechanism of grain quality degradation under high temperature in relation to light conditions (Yoshida and Hara, 1977; Kobata and Uemuki, 2004; Wakamatsu et al., 2009). It is not clear, however, whether temperature responses of different cultivars differ under different growing conditions.

Yield response to temperature is a result of many growth processes and phenotypic traits. Recent studies have highlighted the cultivar differences in reproductive growth processes such as grain set and quality under high temperatures (Matsui et al., 2001; 2005; Tsukaguchi et al., 2011), but our knowledge is still limited on the variation among cultivars in the response of vegetative growth to temperature. Moreover, it is not clear whether any cultivar and growing environment interaction exists in the morphological responses to temperature and its association with growth, which is an important basis for improving the adaptability of cultivars to climate change in a range of conditions. As a consequence, this study was designed to assess the morphological responses —total shoot biomass, panicle biomass and leaf area production— of 18 rice cultivars obtained from different germplasm groups. They were grown under constant day and night temperature of 25, 28, 31 and 34°C in two growth chamber conditions: one with artificial light at Wagga Wagga and the other with natural light at Yanco, NSW, Australia. Consistency or inconsistency of the growth performance among different cultivars in these different types of chambers will provide us with valuable information for adaptation to temperature increases.

Materials and methods

1. Plant cultivar selection

Eighteen rice cultivars with a wide range of heat tolerance were supplied by Yanco Agricultural Institute, NSW Department of Primary Industries, Yanco, NSW, Australia. The cultivar names, germplasm groups, origin

Table 2. Average daily air temperature, relative humidity and vapour pressure deficit measured in conditions under artificially-lit chambers (ALC) in Wagga Wagga and in conditions under naturally-lit chambers (NLC) in Yanco, NSW, Australia, during the two experimental periods (31 and 34°C from September to December 2008 and 25 and 28°C from December to March 2009).

Growing condition	Temperature (°C)			
Temperature setting →	25	28	31	34
ALC	24.6 ± 0.01	26.7 ± 0.03	30.5 ± 0.01	34.8 ± 0.02
NLC	25.0 ± 0.01	28.0 ± 0.01	30.6 ± 0.01	33.7 ± 0.08
	Relative humidity (%)			
Temperature setting →	25	28	31	34
ALC	62.0 ± 0.07	78.4 ± 0.13	51.9 ± 0.09	63.3 ± 0.14
NLC	86.7 ± 0.08	68.0 ± 0.01	nd	nd
	Vapor pressure deficit (kPa)			
Temperature setting →	25	28	31	34
ALC	1.17	1.11	2.09	2.03
NLC	0.42	1.20	nd	nd

± values are standard errors of the means; nd = data not collected.

and level of heat tolerance based on published references are shown in Table 1.

2. Plant growth conditions

An experiment reflecting contrasting growing conditions with different chamber environments was conducted in (1) artificially-lit growth chambers (ALC) located at the Department of Primary Industries (DPI), Agricultural Institute in Wagga Wagga, NSW, Australia, and in (2) naturally-lit growth chambers (NLC) located at the DPI, Yanco, NSW, Australia. At each site, two chambers were used for the two 3-month experimental periods: the first period was from September to December 2008, when the air temperature in each chamber was controlled at 31 and 34°C continuously during day and night, and the second period was from December to March 2009, when the temperature was controlled at 25 and 28°C, respectively. Tinytag data loggers (Omni Instruments Ltd., Scotland, UK) were placed under the pot benches in the middle section of the room to protect from direct light and to record air temperature and relative humidity. Good mixing of the air in the chamber reduced the vertical profile of the air temperature. Relative humidity was not recorded in NLC for the first experimental period due to a lack of instrument. Mean daily vapour pressure deficit was calculated from sowing time until the final harvest at 94 days after sowing (DAS). Settings and conditions in the growth chambers during the experimental period are given in Table 2. Air temperatures measured in the chambers were within the range of ± 1.3°C from the target values averaged over the season (Table 2). Relative humidity was not controlled in this study, which ranged from 52 to 87% across the temperature regimes. The daily vapour pressure deficit was higher at 31°C and 34°C than

at 25°C and 28°C in ALC. Global radiation during the light cycle in ALC measured by Delta T solar energy flux sensor (ES2-05) was 7.8 MJ m^{-2} d^{-1} with 12.5-hr light and 11.5-hr dark setting, and in NLC it was 11.5 MJ m^{-2} d^{-1} during September to December 2008 and 13.4 MJ m^{-2} d^{-1} from December to March 2009, computed as 50% of the average outside light intensity measured at a nearby weather station during the experimental periods. The 50% estimate was based on the actual measurements inside and outside the growth chambers using a Delta-T light meter during the middle of the day in February 2009. In the NLC the average photoperiod for a temperature setting of 31 and 34°C (16 September to 19 December 2008) was 13.5 hours, and for 25 and 28°C (23 December to 27 March 2009) it was 13.4 hr.

In ALC, a fine-textured clay loam soil and in NLC, soil obtained from Yanco in the Murrumbidgee Irrigation Area (MIA) classified as a red-brown earth (Van Dijk, 1961) were thoroughly mixed and transferred into plastic pots (0.16-m diameter × 0.16-m height) until the soil was just below the brim. The pots were placed in stainless steel tanks and wetted for 1 week before sowing. The seed dormancy of each cultivar was broken by placing the seeds in an oven at 50°C for 48 hr. At both locations, the seeds were sown beginning in the first week of September 2008 for the first period, 23 December 2008 in NLC and 11 January 2009 in ALC for the second period. Six seeds were directly sown in each pot; this was done by gently pressing the seeds to about 1-cm depth into the wet soil. In pots in ALC, a complete fertilizer, Thrive, 40 kg N ha^{-1}, 10 kg P ha^{-1} and 15 kg K ha^{-1}, was applied within the first 10 DAS while supplemental N in the form of urea (40 kg ha^{-1}) was applied at 30 and 50 DAS and around flowering, for a total of 160 kg N ha^{-1}. In pots in NLC, 131.13 g of urea (46% N)

Table 3. The main effects of growing conditions, temperature and cultivar and their interactions for total shoot, panicle and leaf biomass measured at 94 DAS.

Growing condition	Temper-ature (°C)	Total shoot biomass (g plant^{-1})			Panicle biomass (g plant^{-1})			Leaf biomass (g plant^{-1})		
		Mean	Minimum	Maximum	Mean	Minimum	Maximum	Mean	Minimum	Maximum
ALC	25	8.3	0.2	13.6	2.0	0.5	3.4	1.91	0.04	4.15
	28	6.9	4.3	16.2	2.3	0.4	4.5	2.13	0.98	4.61
	31	28.2	19.8	43.5	9.8	6.2	14.7	6.06	3.68	15.6
	34	13.5	4.5	27.1	0.4	0.1	1.0	6.36	2.47	12.1
Overall		**14.1**	**7.2**	**25.1**	**3.6**	**1.8**	**5.2**	**4.12**	**1.79**	**9.12**
NLC	25	23.8	15.6	36.9	9.8	5.3	14.3	3.83	2.53	6.14
	28	22.1	16.6	28.2	10.0	7.3	12.9	3.60	2.67	5.52
	31	18.1	9.5	27.3	4.9	0.0	9.2	3.25	1.71	4.90
	34	16.1	3.9	32.6	2.8	0.3	8.9	3.72	1.30	7.24
Overall		**20.0**	**11.4**	**31.2**	**6.9**	**3.2**	**11.3**	**3.60**	**2.05**	**5.95**
ANOVA		*df*	*F*		*df*	*F*		*df*	*F*	
Chamber condition (CC)		1	27.4	***	1	162.7	***	1	8.2	***
Temperature (T)		3	15.0	***	3	76.1	***	3	8.1	***
CC × T		3	32.4	***	3	120.9	***	3	8.1	***
Cultivar (C)		17	9.0	***	17	3.2	**	17	16.7	***
CC × C		17	1.1	ns	16	1.2	ns	17	3.4	***
T × C		51	1.9	**	49	2.1	**	51	3.2	***
CC × T × C		50	1.2	ns	36	1.6	ns	50	2.1	***

, * indicate significance at the 1% and 0.1% levels, respectively. ns, not significant.

was mixed into 3 litres of water, and 10 mL per pot was applied onto the soil surface at 10 DAS: equivalent to 100 kg N ha^{-1}. The timings and amounts of nitrogen fertilizer differed between ALC and NLC applied according to the soil fertility as commonly used at each site.

At the 3-leaf stage, the plants were thinned to two per pot. After taking one plant for the first sampling at 30 DAS, the pot-growing process continued with one.

3. Plant measurements

The plants were sampled for green leaf area and shoot biomass at 30, 49, 72 and 94 DAS, and panicle biomass at 94 DAS. Green leaf area was measured using a leaf area meter, LI-COR Model LI-3100. Biomass was determined after drying it under 70°C for more than 2 days. The specific leaf area was computed as leaf area divided by leaf dry biomass.

4. Data analysis

The data were analyzed by the Statistical Analysis System (SAS, 1995) using the Combined Mixed Model analysis with chamber and temperature conditions as the main factors and cultivar as the split-plot factor. The Tukey-Kramer method was used for multiple comparisons.
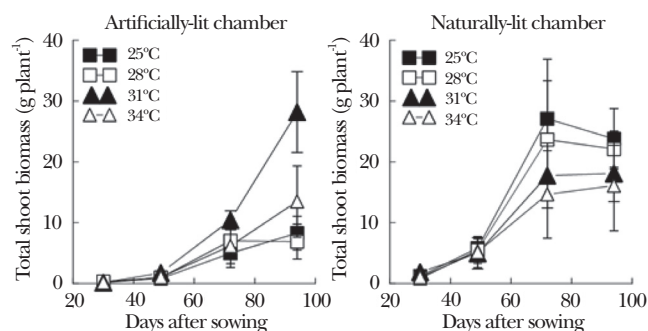

Fig. 1. Changes in total shoot biomass with days after sowing in conditions under ALC (left) and in conditions under NLC (right).

Results

1. Main effects of chamber condition and temperature on growth parameters

Averaged over all the temperature regimes, the total shoot biomass and panicle biomass were heavier ($P < 0.001$, Table 3) in the conditions under NLC than in the conditions under ALC by 29.5% and 47.8%, respectively. A significant interaction between chamber condition and temperature existed for both total shoot biomass and panicle biomass measured at 94 DAS; they were heaviest at

31ºC in ALC (Table 3, Fig. 1, left) and at 25 and 28ºC in NLC (Fig. 1, right). A common observation across ALC and NLC was that a temperature increase from 31 to 34ºC decreased both mean total shoot and panicle biomass (Table 3).

2. Cultivar differences in growth reponse to temperature

The main effect of cultivar was highly significant ($P < 0.001$) and its interaction with temperature was also significant ($P < 0.01$) for total shoot biomass, panicle biomass and leaf biomass (Table 3). The difference in total shoot biomass averaged over two chamber conditions between cultivars was more pronounced at 31 and 34ºC than at 25 and 28ºC (Table 4). The varietal range of panicle biomass averaged over two chamber conditions was the largest at 31ºC (Table 5). No significant interaction between cultivar and chamber conditions for total shoot and panicle biomass suggested that the comparison of cultivars at each temperature was similar across ALC and NLC. In fact, total shoot biomass at ALC and NLC was significantly and positively correlated (Fig. 2, a, b). It is also worth noting that cultivars that performed better at 31ºC also performed well at 34ºC, as evidenced by the significant correlation in Fig. 2 (c) ($P < 0.01$).

The total shoot biomass of each cultivar averaged over two chamber conditions ranged from 16.0 g plant^{-1} in Langi to 35.0 g plant^{-1} in IR72 at 31ºC, and from 4.2 g plant^{-1} in Langi to 29.9 g plant^{-1} in IR64 at 34ºC (Table 4). In contrast, there were no significant differences in total shoot biomass among cultivars at lower temperatures of 25 and 28ºC (Table 4). Among the 18 cultivars, IR64, IR72, Vandana, Takanari, Koshihikari and N22 commonly had higher total shoot biomass at 31 and 34ºC.

In the pooled chamber conditions, the panicle biomass was generally small at 25, 28 and 34ºC and it was higher at 31ºC ($P < 0.001$, Table 5). There were significant differences among cultivars at 31ºC resulting in a significant interaction between temperature and cultivar ($P < 0.01$, Table 3). At this temperature, the panicle biomass ranged from 4.74 g plant^{-1} in IR64 to 10.1 g plant^{-1} in M103, and it was larger in M103, N22 and Vandana. We note here that the cultivars that had a relatively large panicle biomass could be generally early in development, so that they had longer duration for panicle biomass accumulation than did later cultivars or those cultivars with a smaller panicle biomass had their grain setting severely disturbed by high temperatures so that biomass accumulation in the panicle was limited (Table 5). This then represented the differences in phenology and cultivar tolerance of temperature.

Table 4. Total shoot biomass (g plant^{-1}) of 18 individual cultivars measured at 94 DAS under four temperatures from 25 to 34ºC. The values are averages of two growing conditions because there was no significant growing condition and cultivar interaction (Table 3).

Cultivar	25ºC	28ºC	31ºC	Rank	34ºC	Rank
1. Akihikari	14.5 [†]a	13.7 a	19.9 bc	14[‡]	12.1 bcde	13
2. Akitakomachi	14.4 a	16.5 a	22.3 abc	8	7.9 cde	15
3. Amaroo	15.3 a	13.5 a	21.7 abc	12	6.5 de	17
4. Calrose	13.4 a	19.1 a	22.0 abc	11	10.3 bcde	14
5. Cocodrie	13.0 a	11.8 a	19.9 bc	13	15.0 bcde	8
6. Cypress	15.2 a	17.8 a	nd	18	13.8 bcde	11
7. IR64	17.9 a	17.4 a	29.8 ab	2	29.9 a	1
8. IR72	21.3 a	19.1 a	35.0 a	1	19.8 abcd	4
9. Jefferson	14.9 a	15.0 a	16.7 bc	16	13.1 bcde	12
10. Koshihikari	17.4 a	13.7 a	23.2 abc	5	17.7 abcde	5
11. Langi	14.6 a	13.0 a	16.0 c	17	4.2 e	18
12. Lemont	16.8 a	18.1 a	22.3 abc	9	16.3 abcde	6
13. M103	15.6 a	15.5 a	22.2 abc	10	7.3 de	16
14. N22	17.9 a	20.6 a	28.2 abc	4	14.2 bcde	9
15. Nipponbare	13.4 a	12.2 a	22.3 abc	7	15.1 bcde	7
16. Takanari	16.8 a	15.6 a	22.8 abc	6	21.0 abc	3
17. Vandana	22.9 a	17.1 a	29.7 abc	3	21.9 ab	2
18. WAB 450-I-B-P-38-HB	13.4 a	13.9 a	18.8 bc	15	14.2 bcde	10

[†] In a column within each temperature treatment, values followed by a common small letter are not significantly different at 5% level of probability by the Tukey-Kramer method. [‡] Ranks of the cultivars are shown for the temperature regime that showed significant differences among the cultivars.

Table 5.   Panicle biomass of 18 individual cultivars measured at 94 DAS under four temperatures from 25 to 34°C. The values are averages of two growing conditions because there was no significant growing condition and cultivar interaction (Table 3).

Cultivar	25°C	28°C	31°C	Rank	34°C
1. Akihikari	3.42 a[†]	1.27 a	7.25 ab	7[‡]	1.59 a
2. Akitakomachi	3.78 a	1.86 a	7.43 ab	5	0.32 a
3. Amaroo	2.11 a	1.80 a	7.14 ab	8	0.40 a
4. Calrose	3.03 a	2.00 a	7.33 ab	6	0.60 a
5. Cocodrie	5.41 a	6.46 a	7.88 ab	4	0.85 a
6. Cypress	5.53 a	7.71 a	nd	18	0.51 a
7. IR64	3.82 a	4.45 a	4.74 ab	16	3.63 a
8. IR72	2.41 a	3.77 a	nd	17	1.31 a
9. Jefferson	6.68 a	7.65 a	5.82 ab	15	1.10 a
10. Koshihikari	7.21 a	5.41 a	6.04 ab	13	0.68 a
11. Langi	5.69 a	6.25 a	6.07 ab	12	nd
12. Lemont	5.88 a	7.08 a	7.09 ab	9	0.28 a
13. M103	8.08 a	6.41 a	10.13 a	1	0.55 a
14. N22	6.78 a	7.72 a	9.71 a	2	0.54 a
15. Nippon Bare	5.30 a	4.11 a	6.64 ab	11	1.58 a
16. Takanari	7.21 a	4.68 a	6.89 ab	10	4.47 a
17. Vandana	7.03 a	6.02 a	9.52 a	3	3.84 a
18. WAB 450-I-B-P-38-HB	4.67 a	6.46 a	6.02 ab	14	0.57 a

[†] In a column within each temperature treatment, values followed by a common small letter are not significantly different at 5% level of probability by the Tukey-Kramer method. [‡] Ranks are shown for each temperature with significant differences among cultivars.
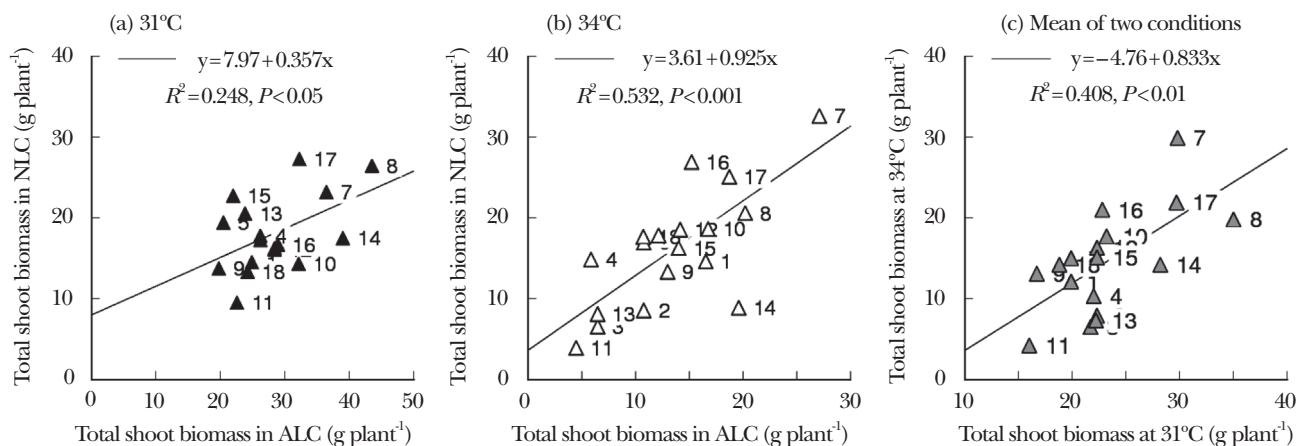

Fig. 2.   Relationships of total shoot biomass of individual cultivars between NLC and ALC at 31°C (a) and 34°C (b). Total shoot biomass at 31 and 34°C was compared using the mean of ALC and NLC for each cultivar (c).

3.   Correlation of early period total shoot biomass, leaf area and specific leaf area with final total shoot biomass

To examine morphological traits associated with differences in final total shoot biomass, we performed a simple correlation analysis by comparing the final total shoot biomass (at 94 DAS) and leaf area, specific leaf area and total shoot biomass at 30, 49 and 72 DAS (Table 6). None of the leaf area, specific leaf area and early total shoot biomass at 25 and 28°C in the conditions under ALC had a significant correlation with final total shoot biomass. This was in agreement with the non-significant difference in the total shoot biomass among individual cultivars under these temperature and chamber conditions (Table 4). Rather, in the conditions under ALC, the leaf area at 31 and 34°C during 49 and 72 DAS was highly correlated with the final shoot biomass, suggesting enhancement and an

Table 6. Correlation coefficients of the relationships between total shoot biomass, leaf area and specific leaf area measured at earlier stages during the crop period with final shoot biomass at 94 DAS obtained from ALC and NLC under four temperatures from 25 to 34°C.

Experiment	Temperature (°C)	DAS	Total shoot biomass			Leaf area		Specific leaf area	
			30	49	72	49	72	49	72
ALC	25		0.34 ns	0.44 ns	0.17 ns	0.35 ns	0.25 ns	0.18 ns	−0.08 ns
	28		0.14 ns	−0.05 ns	0.13 ns	0.30 ns	0.02 ns	0.45 ns	0.19 ns
	31		0.14 ns	0.06 ns	0.06 ns	0.63 **	0.65 **	0.45 ns	0.57 *
	34		0.47 ns	0.65 **	0.85 ***	0.80 ***	0.81 ***	0.54 *	0.54 *
NLC	25		−0.28 ns	0.08 ns	0.30 ns	0.03 ns	0.29 ns	−0.06 ns	−0.01 ns
	28		0.22 ns	0.19 ns	0.52 *	0.38 ns	0.75 ***	0.31 ns	0.40 ns
	31		0.22 ns	0.12 ns	0.76 ***	0.37 ns	0.56 *	0.17 ns	0.07 ns
	34		0.46 ns	0.37 ns	0.73 ***	0.47 ns	0.74 ***	0.59 *	0.62 **

*, **, *** indicate that the correlation coefficients are significantly different from 0 at the 5%, 1% and 0.1% significance levels, respectively. ns, not significant. No leaf area and specific leaf area measurements at 30 days after sowing.

ability to support leaf expansion under high temperatures. On the other hand, in the conditions under NLC, the correlation between leaf area and final total shoot biomass was significant at 72 DAS, at all temperatures except 25°C.

Discussion

The two types of chambers we used in this study differed not only in light intensity but also in light duration; we set daylength as unchanged for the whole experimental period in ALC, whereas daylength in NLC changes daily, although the averaged daylengths were similar. We set constant temperatures throughout the day for each treatment, which is unrealistic compared to the natural fluctuation. These could influence the phenology and development of the plants. The effects on phenology were not negligible so some cultivars failed to complete their life cycle, so our comparison focused mainly on total shoot biomass. For pot cultures, we used a different N rate, for which we used lower amouts for NLC than for ALC, based on soil fertility as commonly used at each site. These factors could have strong influences on cultivar performance. Nevertheless, the present study revealed some consistent effects across two types of chambers, which can be a robust basis for developing adaptation strategy.

1. The main effects of growing conditions and temperature on morphological traits of rice

The total shoot biomass averaged across four temperature regimes was lower in ALC than in NLC by about 30% (Table 3). Multiple factors can be associated with this difference, but a lower light intensity in ALC (by about 37%) can largely account for this. The optimum temperature was lower in the conditions under NLC and it was higher in the conditions under ALC. This resulted in a significant interaction between chamber conditions and temperature (Table 3). It should be noted that, in NLC, light intensity for 25 and 28°C treatments was about 16%

higher than for 31 and 34°C, which might have affected the temperature responses in NLC. A light intensity and temperature combination optimum for growth as observed in the present study was similarly observed by Venkateswarlu and Visperas (1987). Solar radiation of $14.6 - 18.8$ MJ m^{-2} d^{-1} and average daily temperature of $28 - 32$°C produced the most favourable growth and productivity whereas, lower solar radiation ($6.28 - 8.37$ MJ m^{-2} d^{-1}) and average daily temperature of $25 - 30$°C and either high or low light intensity and average daily temperature of $35 - 42$°C suppressed rice growth and productivity (Venkateswarlu and Visperas, 1987). The present observations and those of others confirmed that a strong interaction exists between light intensity and temperature that can affect rice growth and yield, thus requiring more detailed studies on the processes contributing to these effects.

2. Response of individual cultivars to chamber conditions and temperature

The large differences in the pooled total shoot biomass for the two chamber conditions at the higher temperatures of 31 and 34°C caused the significant temperature and cultivar interaction. At these temperatures the consistent higher total shoot biomass in IR64, IR72, N22 (all *indica*), Vandana (*aus/japonica*), Takanari (*tongil or indica/japonica*) and Koshihikari (*japonica*) (Table 4) showed that the production of higher total shoot biomass at a higher temperature was not dependent on a specific germplasm group but rather some specific cultivars were more adapted. N22 was one of those cultivars that ranked higher in total shoot biomass at 31°C (No.4) but ranked lower at 34°C (No.9) in the present study. So far, N22 (Prasad et al., 2006) and Akitakomachi (Matsui et al., 2001) are considered the most heat-tolerant cultivars to date in terms of spikelet fertility among *indica* and *japonica* species, respectively. However, Akitakomachi appeared less adapted

to the conditions of the present study, with total shoot biomass ranking No.8 and No.15 at 31 and 34°C, respectively.

The response of panicle biomass was inconsistent with final total shoot biomass since complex processes are involved when considering phenology and tolerance of temperature among the different cultivars. This response was more distinctly observed at the fixed sampling date in the current study at 94 DAS than it would have been at maturity. The cultivars that developed a larger panicle biomass earlier at 31°C (M103, N22 and Vandana) could either be short duration or their panicle development was positively affected by this temperature, whereas those that have smaller panicle biomass (IR72, IR64, Jefferson) could either be long duration and will still develop grains later or their fertilization was already negatively affected by the high temperature and they will not produce mature grains at all. This is why we have confined our discussion to total shoot biomass but, in future studies, we will consider the whole life cycle to evaluate the economic yield of the rice cultivars.

3. Correlation between total shoot biomass, leaf area and specific leaf area at early measurement dates and total shoot biomass at the final sampling

In ALC, the observed dependence of final total shoot biomass on leaf area as early as 49 DAS at temperatures of 31 and 34°C confirmed the strong response to higher temperature at lower light intensity (Table 6). This was observed at a much earlier date than in NLC (at 72 DAS). Despite the differences in the period of occurrence of the significant correlation between total shoot biomass and leaf area in both chamber conditions, this highlighted that cultivars with a larger leaf area will in general have a larger final total shoot biomass (Table 6). This was observed in widely spaced individual plants as in the present study showing the ability to expand leaves at a high temperature in contrast to the commonly observed negative correlation between leaf area and biomass in the field with full canopy due to a shading effect. This was possible since a large leaf area will allow greater whole-plant photosynthesis if combined with higher rate of photosynthesis per unit leaf area (Sheehy et al., 2008). This then indicates that conditions that encourage leaf area expansion will increase total shoot biomass production and should enhance potential grain yield as long as temperature has no further effect on the reproductive development of the rice plant. In past field studies, linear regression analysis showed a high correlation between final grain yield and leaf area index of plants at 28 DAS for an inbred rice genotype (IR72) in the dry season ($P = 0.055$) and in a hybrid rice genotype (IR75217H) in the wet season ($P = 0.05$) (Pasuquin et al., 2008).

Conclusions

Chamber conditions interacted with temperature in affecting total shoot biomass and leaf area production. The conditions in ALC and at 31°C, and in NLC and at 25 and 28°C were the most favourable for total shoot biomass and leaf area production. In separate and pooled chamber conditions, IR64, IR72, N22, Vandana, Takanari and Koshihikari produced higher total shoot biomass at 31 and 34°C and this was correlated more with higher leaf area than specific leaf area. This study was conducted in pots in growth chamber conditions where relative humidity was not controlled. Therefore, further experimentation in environments where either temperature or relative humidity or both can be controlled are justified and are the subject of our following studies.

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