Crop and Environment 2 (2023) 147–156

Contents lists available at ScienceDirect

Crop and Environment

journal homepage: www.journals.elsevier.com/crop-and-environment

Original Article

Responses to elevated daytime air and canopy temperature during panicle development in four rice genotypes under paddy conditions in large field chambers

Estela M. Pasuquin [a,b], Philip L. Eberbach [a], Toshihiro Hasegawa [c], Tanguy Lafarge [d], Dome Harnpichitvitaya [e], Len J. Wade [f,*]

[a] Graham Centre for Agricultural Innovation, School of Agricultural Environmental and Veterinary Sciences, Charles Sturt University, Locked Bag 588, Wagga Wagga NSW 2678, Australia
[b] Crop and Environmental Sciences Division, International Rice Research Institute, DAPO Box 7777, Metro Manila, Philippines
[c] Institute for Agro-Environmental Sciences, National Agriculture and Food Research Organization, Tsukuba, Ibaraki 305-8604, Japan
[d] CIRAD (Centre International de Recherche en Agronomie pour le Développement), UMRAGAP F-34398, Montpellier, France
[e] Department of Agronomy, Ubon Ratchathani Rajabhat University, Ubon Ratchathani, Thailand
[f] School of Agriculture and Food Sciences, University of Queensland, Brisbane QLD 4072, Australia

ARTICLE INFO

Keywords:
Ambient and elevated temperature
Canopy cooling
Leaf gas exchange
Spikelet fertility
Yield potential

ABSTRACT

Rising air temperatures have the capacity to impact rice yields in future climates. Studies in large temperature-controlled field chambers were established to examine the responses of four contrasting rice genotypes to elevated daytime temperatures (ET) during reproductive development under paddy conditions. Field chambers were effective in raising mean above-canopy maximum daytime temperatures from 29.9 to 41.1°C during 12 d of ET treatment (68–80 d after emergence, DAE), while increased transpiration under ET resulted in lowering of mean lower-canopy maximum temperature to 33.2°C. Nevertheless, the earliest genotype Vandana encountered a hot spell of 37.0°C at 68–74 DAE in the lower canopy at its late reproductive stage, which exceeded the spikelet sterility threshold of 33.7°C, so its spikelet fertility, grain number and grain yield were reduced under ET. Genotypes differed in the extent of canopy cooling, with less reduction in Vandana and IR64 than in N22 and Takanari. For canopy cooling to be effective, stratification of air layers must occur within the canopy, which was more effective under the shorter and denser canopy of N22 and Takanari (plant height of 70–80 cm) than under IR64 (90–110 cm) and Vandana (115–130 cm). Genotypes with appropriate canopy structures should be chosen for high vapour pressure deficit (VPD) conditions. Both maximum canopy temperature and VPD need to be specified to define the critical threshold for heat tolerance. Takanari was notable for greater leaf area retention and greater leaf photosynthetic capacity due to the maintenance of a higher internal leaf CO_2 concentration, which led to higher spikelet and grain numbers and higher yield potential under ET conditions.

1. Introduction

Rising levels of greenhouse gases in the atmosphere will further increase air temperature over the next century. On a global scale, there has been an upward trend in average annual maximum temperature (Zwiers et al., 2011), as well as increased intensity and frequency of heat waves, droughts and floods (IPCC, 2012). Recent projections from climate-prediction models indicate an increase in global surface temperature between 0.3 and 4.8°C from 1986–2005 levels by 2100, dependent upon the Representative Concentration Pathway used for the simulation (IPCC, 2013). Anticipated increases in global annual maximum atmospheric temperature between 1.5 and 2.0°C, as agreed at the United Nations Framework Convention on Climate Change (UNFCCC) 2015 negotiations in Paris, have the potential to impact agricultural production across the globe.

Rice, one of the world's major cereal crops, forms the basis of the daily diet for about 3 billion people worldwide (Fairhurst and Dobermann, 2002), but is vulnerable to the impacts of climate change

* Corresponding author.
E-mail address: len.wade@uq.edu.au (L.J. Wade).

https://doi.org/10.1016/j.crope.2023.04.004
Received 4 November 2022; Received in revised form 28 April 2023; Accepted 28 April 2023

(Wassmann et al., 2009a). Rice is sensitive to high temperature during the reproductive phase, as well as in the grain filling period (Yoshida, 1981). In rice-growing areas in which grain filling and maturation coincide with the hottest periods of the year, rice yield (Wassmann et al., 2009a) and grain quality (Krishnan et al., 2011) are expected to be adversely affected. Vulnerable areas extend from the low-latitude tropics to mid-latitude temperate regions (Wassmann et al., 2009b).

Under controlled-environment conditions, when day/night temperatures were raised from 28.3/21.3 to 33.1/27.3°C, spikelet fertility decreased in several rice cultivars (Prasad et al., 2006), and this was attributed to decreased pollen production and decreased pollen reception by the stigma. Exposure to elevated temperature in the 7-d period leading up to anthesis also induced spikelet sterility (Martinez-Eixarch and Ellis, 2015). Processes affecting pollen germination and shedding such as the length of anther dehiscence (Matsui et al., 2005) and the number of viable pollen grains produced (Jagadish et al., 2010; Matsui et al., 2001), generally reduce spikelet fertility, which has been ascribed to a number of high-temperature-induced anomalies: small anther pore size, poor anther dehiscence, low pollen production and viability, poor pollen germination on the stigma and poor pollen tube growth rate (Jagadish et al., 2007, 2008; Martinez-Eixarch and Ellis, 2015; Matsui et al., 2001; Matsui and Omasa, 2002; Prasad et al., 2006). Overall, periods of high temperature occurring before or during anthesis have detrimental effects on pollen number, resulting in elevated levels of sterility in rice spikelets, with 33.7°C considered the threshold temperature (Jagadish et al., 2007).

Environmental parameters also interact to affect spikelet sterility. In a study investigating the effects of relative humidity (RH) on temperature-induced sterility in rice, an RH of 85% increased spikelet sterility as temperature increased beyond 34°C (Weerakoon et al., 2008), which was consistent with a threshold of 33.7°C (Jagadish et al., 2007). In the field, under humid and windless conditions in central China, Tian et al. (2010) showed that air temperatures of 32–33°C during anthesis led to severe spikelet sterility in rice. Against this background, rice genotypes have been reported to differ in heat tolerance, from very sensitive to very tolerant (Jagadish et al., 2008; Matsui et al., 2005; Pasuquin et al., 2013; Prasad et al., 2006; Takai et al., 2006).

Conversely, field data from southern Australia showed that floret fertility in rice grown under irrigated paddy conditions was unaffected by maximum daytime temperatures exceeding 40°C during anthesis (Matsui et al., 2007, 2014). Those studies suggested that transpiration lowered canopy air temperature by up to 7.5°C, thereby restraining the increase in air temperature around the developing panicle to levels below the threshold of 33.7°C. The concept of transpiration influencing the temperature of plant organs has previously been demonstrated by Julia and Dingkuhn (2013), who showed temperature within the crop canopy may vary substantially compared to air temperature outside the crop canopy (ranging from −9.5 to 2°C). At issue for spikelet sterility, therefore, is the actual temperature to which the sensitive spikelet tissue is exposed during panicle development. Consequently, it may be important to record not only temperature but also RH and vapour pressure deficit (VPD) within the canopy during spikelet development, in order to more closely relate increase in spikelet sterility to increase in canopy temperature across genotypes and environments.

Hence, studies in large temperature-controlled field chambers were established to examine the responses of four contrasting rice genotypes to elevated daytime temperature during reproductive development under paddy conditions. The objectives were (1) to measure leaf gas exchange, canopy air temperature and transpirational cooling during reproductive development and grain filling under two contrasting temperature regimes and (2) to quantify the responses in rice phenology, growth, spikelet fertility and grain yield to elevated temperature during reproductive development. The implications for desired canopy measurements and genotype characteristics are discussed.

2. Materials and methods

2.1. Field growth chambers, experimental design and treatments

Four large field chambers (7.0 m long, 3.0 m wide, and 3.8 m high) were built during November and December 2009 at the Charles Sturt University farm, Wagga Wagga, NSW, Australia. Each large field chamber was shaped like an inverted cone with a helical fan at the top, which enabled air to exit vertically from each chamber. Each structure was covered with polythene film similar to that used in hoop houses. The sides of each field chamber could be raised up to 1 m to modify internal temperature. When the sides were open, internal conditions in the chamber approximated those outside of the chamber. With careful management, the sides could be adjusted to elevate maximum daytime temperature by around 10°C (Tables 1, 2).

The experimental design was split-plot with two temperature treatments by two replicates as main plots and four rice genotypes as subplots. Field chambers were placed sufficiently far apart so that no shading occurred from one to another. The temperature treatments were ambient (AT) and elevated (ET). The genotypes chosen had been reported to differ in heat tolerance, from very sensitive (*indica* Takanari) to sensitive (*indica* Vandana) and from sensitive-tolerant (*indica* IR64) to very tolerant (*indica* N22) (Jagadish et al., 2008; Matsui et al., 2005; Pasuquin et al., 2013; Prasad et al., 2006; Takai et al., 2006; Table 3). These genotypes also displayed considerable genetic diversity (McNally et al., 2009).

2.2. Treatment establishment and cultural practices

Each field chamber contained six circular plastic tanks, which were placed sufficiently apart so that no shading occurred from one to another. The tanks, each 1.1 m in diameter and 0.5 m deep, were filled with a medium clay-textured red Kandasol soil (Isbell, 2002) to a depth of 0.3 m. A basal dressing of 14 g *Aquasol,* equivalent to 40 kg N ha^{-1}, 7 kg P ha^{-1} and 32 kg K ha^{-1}, was incorporated. The soil was then saturated, cultivated wet (puddled), and kept flooded to a depth of 0.03–0.05 m throughout the experiment, so a consistent hydrology was available for each treatment. Within each field chamber, one tank was planted to each genotype. The two remaining tanks in each field chamber were divided equally, with a single genotype being planted within each half. Rice (IR64) was also planted in the guard areas surrounding the tanks, both inside and outside the field chambers, so the measured plants within each treatment were surrounded by transpiring rice plants throughout.

Table 1
Daily maximum, minimum and mean temperature, relative humidity and vapour pressure deficit before treatment (16–67 DAE), during the temperature treatment period (68–80 DAE) and after the treatment period (81–143 DAE).

	Temperature (°C)			RH (%)			VPD (kPa)		
	Maximum	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean
16–67 DAE	39.6±0.83	17.4±0.45	28.0±0.56	76.0±1.85	19.8±2.02	43.4±2.28	6.35±0.37	0.50±0.04	2.75±0.07
68–80 DAE-AT	29.6±1.55	14.8±1.07	21.4±0.82	90.1±1.86	40.9±6.43	65.8±4.60	2.72±0.42	0.16±0.03	0.90±0.14
68–80 DAE-ET	39.1±2.11	15.6±0.95	24.6±1.10	95.6±0.90	40.8±4.40	72.7±3.35	4.63±0.63	0.07±0.01	0.87±0.12
81–143 DAE	37.8±0.53	11.6±0.43	21.6±0.39	98.0±0.10	29.6±1.60	72.4±0.86	4.76±0.18	0.03±0.00	0.73±0.03

Abrreviations: AT, ambient temperature; ET, elevated temperature; DAE, days after emergence; RH, relative humidity; VPD, vapour pressure deficit. Values are presented in mean±SD.

Table 2
Average maximum temperature (°C) in ambient and elevated temperature treatments for above canopy and lower canopy, and the temperature differences between treatments in above canopy, lower canopy, and between above and lower canopy for four rice genotypes (Vandana, N22, Takanari and IR64) during the temperature treatment period (68-80 DAE).

Genotype	Above canopy			Lower canopy			Above – Lower canopy		
	AT	ET	(ET-AT)	AT	ET	(ET-AT)	AT	ET	(ET-AT)
Vandana	29.6 b	41.0 a	11.4 A	27.5 b	34.3 a	6.8 A	2.2 cd	6.7 b	4.6 B
N22	29.5 b	41.3 a	11.8 A	27.0 b	32.0 a	5.1 BC	2.6 c	9.3 a	6.7 A
Takanari	29.9 b	41.0 a	11.0 A	28.7 b	33.2 a	4.4 C	1.2 d	7.8 b	6.6 A
IR64	30.5 b	41.0 a	10.4 A	27.5 b	33.6 a	6.1 AB	3.1 c	7.4 b	4.3 B
Mean	29.9	41.1	11.2	27.7	33.2	5.6	2.3	7.8	5.6

Abrreviations: AT, ambient temperature; ET, elevated temperature; DAE, days after emergence.
Different lowercase letters for each canopy level represent the significant difference and different uppercase letters within a column represent significant difference according to LSD (0.05).

Table 3
Plant height, heat tolerance and dates of emergence, transplanting, panicle initiation, start and end of temperature treatments, anthesis and maturity of four genotypes (Vandana, N22, Takanari and IR64) at Wagga Wagga in 2010.

Genotype	Height (cm)	Heat tolerance[a]	Emergence date[b] (d)	Transplanting date (d)	Panicle initiation date (d)	Start of elevated temperature	End of elevated temperature	Anthesis date (d)	Maturity date (d)
Vandana	115-130	S	21 Dec (0)	2 Jan (14)	23 Feb (64)	27 Feb (68)	11 Mar (80)	16 Mar (85)	9 Apr (111)
N22	70-80	VT	21 Dec (0)	2 Jan (14)	25 Feb (66)	27 Feb (68)	11 Mar (80)	21 Mar (90)	16 Apr (118)
Takanari	70-80	VS	21 Dec (0)	2 Jan (14)	27 Feb (68)	27 Feb (68)	11 Mar (80)	29 Mar (98)	29 Apr (131)
IR64	90-110	S-T	21 Dec (0)	2 Jan (14)	3 Mar (72)	27 Feb (68)	11 Mar (80)	7 Apr (107)	11 May (143)
Mean			21 Dec (0)	2 Jan (14)	27 Feb (68)	27 Feb (68)	11 Mar (80)	26 Mar (95)	24 Apr (126)

[a] S, susceptible (Jagadish et al., 2008); VT, very tolerant (Prasad et al., 2006); VS, very susceptible (Matsui et al., 2005); S-T, sensitive-tolerant (Jagadish et al 2008).
[b] For all dates, the days after emergence are also shown in parentheses.

Seeds of each genotype were sown on 18 December 2009 into individual plastic germination trays containing a mixture of soil and plant compost (potting mix). After sowing, the trays were placed in shallow metal tanks in a glasshouse set to 26°C and kept saturated. On 2 January 2010, 12 DAE, the seedlings were removed from their trays and transplanted to their randomly-designated plastic tanks at a plant density of 1 seedling hill^{-1} spaced 0.17 × 0.17 m (34.6 plants m^{-2}). There were 32 plants in each single-genotype main tank (maintained in an untouched state for temperature, phenology and final yield measurements), and 16 plants per genotype in each split tank (for destructive shoot and root sampling). Until the temperature treatments commenced, rice was grown at ambient temperature and RH by keeping the sides open. A side-dressing of 12 g of commercial fertilizer *Thrive,* equivalent to 40 kg N ha^{-1}, 8 kg P ha^{-1} and 14 kg K ha^{-1} was done at mid-tillering. Supplemental N fertilizer as urea was applied at a rate of 40 kg N ha^{-1} at heading and anthesis, resulting in a total N-fertilizer equivalent for the rice crop of 160 kg N ha^{-1}. Ponded water was maintained until physiological maturity.

2.3. Temperature treatments and monitoring of air and canopy temperature

On the evening of 26 February 2010, the sides in two of the four large plastic chambers were lowered to elevate the temperature in the elevated temperature (ET) treatment, while the sides in the other two chambers remained open in the ambient temperature (AT) treatment. Despite the sides being lowered in the ET chambers, air could still enter the lower section and move through each chamber to exit through the helical fan mounted at the top of each chamber. At the cessation of the treatment period, the sides in the ET treatments were opened again in the morning of 12 March, and an average daily temperature of 22–23°C was then maintained in all chambers until maturity, by adjusting the sides between 9:00 and 16:00 if needed. Thus, the ET and AT treatment conditions were maintained for a 12-d period, from 27 February to 11 March (68–80 DAE).

Air temperature and RH in the internal environment of each chamber were logged every 10 min using a 4-Channel Hobo data logger (U-12, Onset Bourne, MA, USA), with a sensor installed in the center of each chamber at 1.6 m above the soil surface. The loggers were mounted in slotted radiation shields comprising an open-bottomed 0.12 m plastic pipe which protected the sensor and logger from direct sunlight, but still allowed for adequate natural airflow.

Air temperature at three heights in the canopy was also measured for each genotype in each chamber. Temperature sensors (TMC6-HD 412-006, Onset Bourne, MA, USA) were mounted in slotted radiation shields in the middle of each tank: (1) in the lower canopy (0.10 m above the water surface), (2) in the mid-crop canopy, and (3) above the canopy (immediately above the highest leaf). Each sensor was mounted in the middle of the radiation shield and set adjacent to the slots to ensure good air exchange. Each sensor was connected to the same Hobo data logger which was programmed to record temperature every 10 min. Canopy temperature measurements commenced on 27 February (68 DAE) and continued until 5 April (105 DAE).

2.4. Phenology, growth, grain yield and yield components

Panicle initiation was checked daily on the main tillers of two non-border plants within the split tanks used for destructive sampling by hand-lens inspection of shoot apices, which were recorded as the mean length of the developing panicle (mm). When 50% of reproductive apices had attained 2 mm in length, the treatment was deemed to be at panicle initiation. The first anthesis was recorded when spikelets in panicle tips exhibited anther appearance in 50% of main panicles. Physiological maturity was recorded when grains were firm in panicle bases without milky residues in 50% of main panicles.

Destructive samples, comprising whole plants including roots, were taken from split tanks at the commencement of the temperature treatments at 68 DAE, at the end of the temperature treatments at 80 DAE and at physiological maturity. For each sample, two sets of two non-border plants per genotype (sample area equivalent to 0.06 m^2) were cut at ground level and bagged. In the laboratory, the number of tillers was counted, and plant height and stem length were measured. The green leaves, dead leaves and stems were separated and green leaf area was measured using a leaf area meter (LI-3100, LI-COR, Lincoln, NE, USA). Two soil monoliths, each containing an entire root system of a single

plant per genotype, were also sampled using a metal rectangular soil sampler (0.20 × 0.20 × 0.50 m). In collecting the entire root system, the sampler was centrally positioned over the top of the target root system and pushed into the soil until it encountered the bottom of the tank. The sampler was then carefully removed from the tank, and the roots were washed free of soil and bagged. The green leaves, dead leaves, stems and roots were oven-dried in a fan-forced oven at 70°C for 48 h and their dry weight (DW) was recorded. Specific leaf area (SLA) was calculated as green leaf area divided by green leaf DW, and specific stem length (SSL) was calculated as stem length of the main tiller divided by its stem DW.

Panicles of ten randomly selected non-border plants (sample area equivalent to 0.29 m^2) growing in the main tanks were individually bagged, and the plants were cut from the base and taken to the laboratory. The number of panicles $plant^{-1}$ was counted and the viable (filled) and sterile (unfilled) spikelets $panicle^{-1}$ were separated by palpation and counted. The counted spikelets were oven-dried at 70°C for 48 h and weighed. Percent spikelet fertility was calculated as 100 × number of filled spikelets/total number of spikelets. Mean grain weight, mean DW of grain $plant^{-1}$ and grain yield were also calculated from these panicle samples from the main tanks.

2.5. Leaf gas exchange

Light-saturated net photosynthetic rate (Amax), stomatal conductance (Gs), transpiration rate (Tr) and intercellular CO_2 concentration (Ci) were measured between 11:00 and 15:00 at 68, 75, 80 and 95 DAE with a portable photosynthesis system (LI-6400, LI-COR, Lincoln, NE, USA). The LI-6400 settings were 380 μmol mol^{-1} as CO_2 concentration, 500 μmol s^{-1} as fixed flow rate, 1,800 μmol m^{-2} s^{-1} as photon flux density and 0.6 as stomatal ratio. Block temperature was set to 32°C in both treatments in order to compare the gas exchange capacity of the leaves, as 32°C was the temperature at which maximum rates of photosynthesis were recorded in rice (Nagai and Makino, 2009). Relative humidity in the cuvette reached a maximum of 30% in the AT chamber and 60% in the ET chamber. Measurements were taken on two non-border plants in the inner portion of each main tank, on the penultimate fully-expanded leaf of the main stem. The leaf chamber was clipped to the 2/3 position from the leaf base, and data were logged when Amax and Gs became stable.

2.6. Statistical analysis

Analyses of variance were performed with replicate and temperature tested against main plot error, and genotype and genotype × temperature tested against residual error (SAS, 2008). Means were compared using least significant difference (LSD) for temperature, genotype and temperature by genotype (Steel and Torrie, 1960).

3. Results

3.1. Air and canopy temperature, relative humidity and vapour pressure deficit

Mean daily maximum and minimum air temperature, RH and VPD above the canopy for the duration of the experiment (0–140 DAE) are shown in Appendix 1, with mean values before treatment (16–67 DAE), during treatment (68–80 DAE) and after treatment (81–134 DAE) shown in Table 1. During the treatment period, maximum air temperature in ET averaged 39.1°C, which was similar to values both before and after the treatment period, but was 9.5°C higher than in AT during the treatment period. The maximum VPD in ET during the treatment period was 4.63 kPa, which was similar to VPD after the treatment period, but was 1.91 kPa higher than in AT during the treatment period. Responses to ET in minimum air temperature and RH were smaller (0.8°C and 5.5%, respectively). After treatment (81–134 DAE), the minimum air temperature averaged only 11.6°C (Table 1).

Mean maximum canopy temperature in AT and ET during the treatment period (68–80 DAE) for above canopy, lower canopy and differences between them are summarised for four genotypes in Table 2, with the typical diurnal temperature pattern in AT and ET shown in Fig. S1, trends for gain in temperature, RH and VPD (ET minus AT) during the treatment period shown in Fig. S2, and trends in differences in temperature between above- and mid-canopy, and between above- and lower-canopy shown in Figs. S3 and S4, respectively. Over the 12-d period treatment, mean maximum above-canopy temperature in ET was 41.1°C, which was 11.2°C higher than in AT (Table 2). In contrast, the mean maximum lower-canopy temperature in ET was 33.2°C, which was 5.6°C higher than in AT. Canopy cooling in the lower canopy of ET relative to its above canopy temperature was 7.8°C, compared with only 2.3°C in AT. Consequently, during the treatment period, canopy temperature decreased from above-canopy to mid-canopy to lower-canopy, and with larger reductions under ET (Fig. S1–S4). Genotypes differed in the extent of canopy cooling (above-canopy minus lower-canopy, Table 2) with less overall reduction in IR64 and Vandana (4.3°C and 4.6°C, respectively) than in Takanari and N22 (6.6 and 6.7°C, respectively).

3.2. Rice phenology and its relationship with temperature, RH and VPD in the field chambers

Genotypes were similar in the timing of panicle initiation at about 68 DAE, with Vandana and N22 being 4 and 2 d earlier than Takanari, and IR64 being 4 d later (Table 3). Thereafter, these small differences continued to diverge, so anthesis occurred at 85 d in Vandana, 90 d in N22, 98 d in Takanari and 107 d in IR64, and physiological maturity occurred at 111 d in Vandana, 118 d in N22, 131 d in Takanari and 143 d in IR64. N22 and Takanari were short in stature (70–80 cm), while IR64 and Vandana were tall (90–110 and 115–130 cm, respectively).

Maximum air and lower-canopy temperature during the reproductive stage, and minimum air and lower-canopy temperature during grain filling, are presented for a 6-d period from panicle initiation to maturity, relative to phenological development in the four rice genotypes (Tables 4, 5). These 6-d periods captured significant natural fluctuation in external air temperature, especially during the 12-d period of ET (68–74 vs. 74–80 DAE, Appendix 1). Under ET from 68 to 74 DAE, the higher above-canopy maximum (43.7°C), and especially the higher lower-canopy maximum temperature (37.0°C), coincided with the later stages of spikelet development in the earlier genotypes, Vandana and N22, but not in the later genotypes. Conversely, lower minimum temperature late in the life cycle affected grain filling in the later genotypes, with N22 encountering minimum temperatures of 10.0°C from 110 to 116 DAE, Takanari of 12.6 to 10°C from 110 to 128 DAE and IR64 of 12.6 to 8.7°C throughout its grain filling (110–140 DAE).

3.3. Rice growth and grain weight component responses to the temperature treatments

Before the imposition of the temperature treatments (68 DAE), total DW in Takanari was significantly lower than in other genotypes (Fig. 1), which was associated with fewer tillers, smaller leaf area, shorter stem length and lower stem DW (Table S1). By the end of the treatment period (80 DAE), Takanari had lower total DW than other genotypes due to fewer tillers and lower stem DW. The late genotypes Takanari and IR64 had lower stem DW, and Takanari had lower dead leaf DW. At maturity, N22 had a greater total DW than Vandana and IR64, with Takanari intermediate. Takanari had the highest green leaf area at maturity, despite its lower tiller number and SLA.

Because genotypes differed in phenology (Table 3) and in plant size at the commencement of the temperature treatments (Fig. 1), changes in crop parameters were examined during the treatment period (68–80 DAE), after the treatment period (80–144 DAE) and combined over both periods (68–144 DAE) (Fig. 2, Table S2). During treatment, leaf area was unchanged in Vandana (−14 cm^2 $plant^{-1}$), but increased significantly in other genotypes (507 cm^2 $plant^{-1}$), especially in Takanari and N22 (752 cm^2 $plant^{-1}$) under AT and in IR64 (579 cm^2 pl^{-1}) under ET (Fig. 2A).

Table 4
Above-canopy and lower-canopy maximum temperature during the reproductive stage and minimum temperature during the grain filling stage for a 6-d period in two temperature regime treatments.

Temperature regime	Maximum temperature (°C)							Minimum temperature (°C)						
	62-68 DAE	68-74 DAE	74-80 DAE	80-86 DAE	86-92 DAE	92-98 DAE	98-104 DAE	104-110 DAE	110-116 DAE	116-122 DAE	122-128 DAE	128-134 DAE	134-140 DAE	140-146 DAE
ET above	35.2	43.7	35.5	37.5	38.4	37.8	36.3	13.2	8.9	11.2	11.8	8.1	8.1	8.0
ET lower	32.6	37.0	29.7	31.2	33.1	30.9	29.9	14.0	10.0	12.1	12.6	8.9	8.8	8.6
AT above	32.6	31.8	28.1	33.5	38.0	37.0	35.0	13.3	9.0	11.2	11.8	8.0	8.0	7.9
AT lower	31.5	30.0	26.9	29.6	32.3	31.3	30.1	14.1	10.0	12.0	12.6	9.0	8.9	8.7

Abbreviations: AT, ambient temperature; ET, elevated temperature; DAE, days after emergence.

Table 5
Phenological development of four rice genotypes (Vandana, N22, Takanari and IR64) exposed to elevated temperature treatment from 68 to 80 days after emergence (DAE).

Genotype	DAE													
	62-68 DAE	68-74 DAE	74-80 DAE	80-86 DAE	86-92 DAE	92-98 DAE	98-104 DAE	104-110 DAE	110-116 DAE	116-122 DAE	122-128 DAE	128-134 DAE	134-140 DAE	140-146 DAE
Vandana	64[a]	H[b]		85					111					
N22	66	H			90				L	118				
Takanari		68	H			98			L	L	L	131		
IR64		72	H					107	L	L	L	L	L	143

[a] Reproductive stage commenced at panicle initiation with 64, 66, 68 and 72 DAE; reproductive stage ceased and grain filling commenced at anthesis with 85, 90, 98 and 107 DAE; and grain filling ceased at physiological maturity with 111, 118, 131 and 143 DAE for four genotypes.
[b] H and L indicated a 6-d period in which genotypes were exposed to high and low temperatures, respectively.

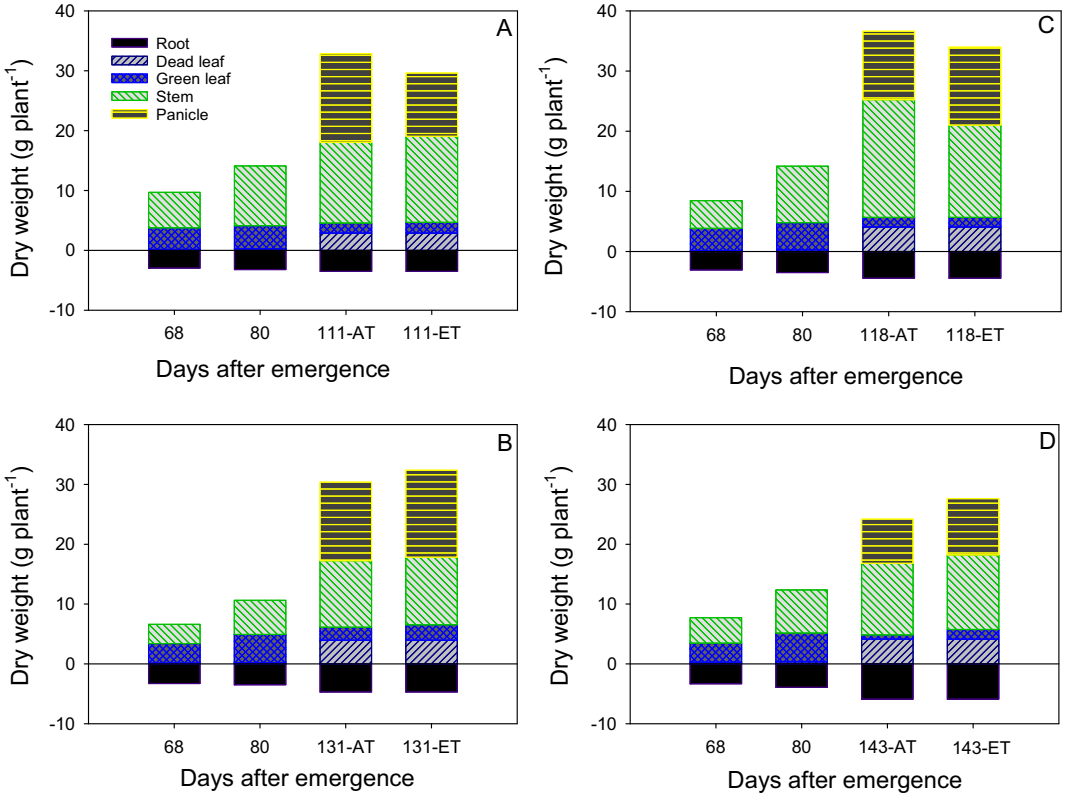

Fig. 1. Aboveground (dead leaf, green leaf, stem and panicle) and belowground (root) allocation of dry weight before treatment (68 day after emergence, DAE), at the end of the treatment period (80 DAE) and at maturity for both ambient temperature (AT) and elevated temperature (ET) in four rice genotypes of (A) Vandana, (B) Takanari, (C) N22 and (D) IR64. LSD for each parameter at each sampling time is presented in Table S1.

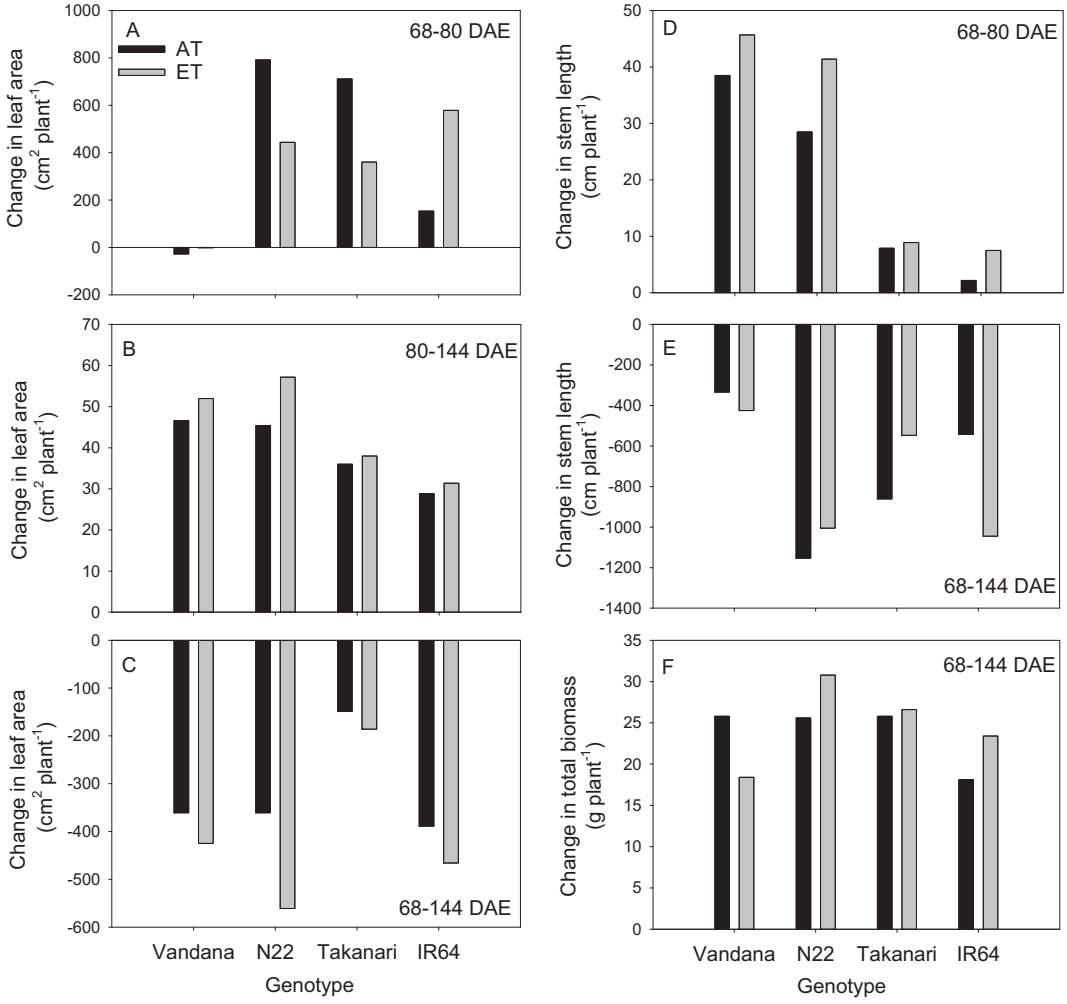

Fig. 2. Changes in leaf area (A) during the treatment period (68–80 day after emergence, DAE), (B) during the post-treatment period (80–143 DAE), and (C) combined over both treatment and post-treatment periods (68–143 DAE). Changes in stem length (D) during the treatment period (68–80 DAE) and (E) combined over both treatment and post-treatment periods (68–143 DAE), and (F) changes in total biomass combined over both treatment and post-treatment periods (68–143 DAE). Data were for four rice genotypes (Vandana, N22, Takanari and IR64) under ambient temperature (AT) and elevated temperature (ET). LSD for genotype × temperature ($P < 0.10$) were 391, 391, 181, 8.7, 7.8 and 7.0 for parameters in A-F, respectively. Further details are presented in Table S1.

After the treatment period, leaf area decreased in all genotypes (−739 cm^2 $plant^{-1}$), especially in N22 in both temperature regimes, in Takanari under AT, and in IR64 under ET (Fig. 2B). When combined, however, the reduction in leaf area was less in Takanari (−168 cm^2 $plant^{-1}$) than in the other genotypes (−430 cm^2 $plant^{-1}$), and leaf area decreased to a greater extent in N22 under ET (Fig. 2C). Early genotypes Vandana and N22 increased more in stem length during treatment (Fig. 2D) and overall (Fig. 2E), especially under ET, while late genotypes increased more in stem length after treatment (Fig. 2E). When combined over both periods, total DW increased to a similar extent on average over temperature regimes (24.3 g $plant^{-1}$), with a lesser increase in Vandana under ET and in IR64 under AT (Fig. 2F).

Yield components at maturity are presented in Fig. 3 and Supplementary Table 3. The statistical analysis identified and replaced two outliers (Replication 4 of Vandana and N22 under AT) for grain DW $plant^{-1}$, spikelets $plant^{-1}$, grains $plant^{-1}$ and harvest index. Why these values were outliers is not known. Spikelets $plant^{-1}$ were high in Takanari and N22 and low in Vandana and IR64 (Fig. 3A). Spikelet fertility percentage was reduced in Vandana under ET and was lower under both AT and ET in IR64 (Fig. 3B). Consequently, grains $plant^{-1}$ were lower in Vandana under ET and in IR64 under both temperature regimes (Fig. 3C). Vandana and IR64 had larger individual grain weight than Takanari and N22 (Fig. 3D). Harvest index was lower in IR64, especially under AT (Fig. 3E). Grain yield decreased in Vandana under ET and was low in both regimes in IR64 (Fig. 3F).

3.4. *Leaf gas exchange*

Before the imposition of the temperature treatments (68 DAE), Takanari had higher Amax and Tr than other genotypes, while Vandana was lower in Ci and Gs (Table S4). Tr and Gs were significantly higher under ET (75 DAE), as were Amax and Ci, but to a lesser extent. After 12 d of treatment (80 DAE), parameter values were still generally greater under ET. Under AT, Takanari had significantly larger Tr and Gs than other genotypes. By 95 DAE (15 d after cessation of treatment), the response to ET in Gs and Tr was smaller than during the treatment period, while Takanari and IR64 had generally higher parameter values than Vandana and N22. General relationships among the gas exchange parameters over all genotypes, treatments and sampling times are shown in Fig. 4. Amax increased linearly with Tr up to 12 mmol m^{-2} s^{-1}, and then plateaued as Tr increased further (Fig. 4A). The response of Takanari was steeper and plateaued higher at 30 μmol m^{-2} s^{-1}, while the slope of N22 was flatter with a lower plateau of 22.5 μmol m^{-2} s^{-1}, and Vandana and IR64 were intermediate. In contrast, the relationship between Tr and Gs was almost linear and consistent over genotypes (Fig. 4B). Although data were more widely spread for Amax versus Ci, data for Takanari were in

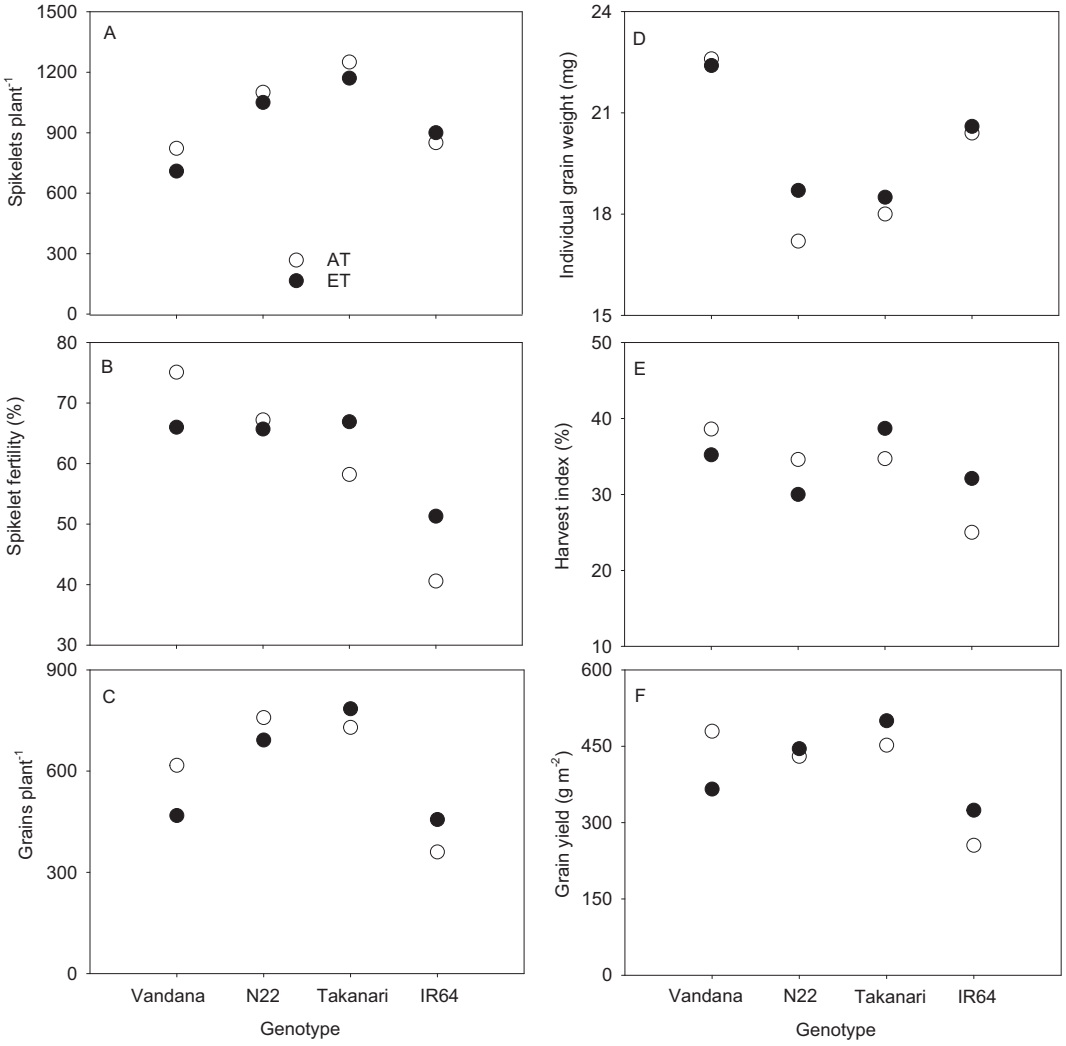

Fig. 3. Yield components at maturity for four rice genotypes (Vandana, N22, Takanari and IR64) under ambient temperature (AT) and elevated temperature (ET). LSD for genotype × temperature ($P < 0.10$) were 194, 13.6, 148, 1.1, 5.4 and 2.8 for parameters in A-F, respectively. Further details are presented in Table S3.

the upper-right quadrant with higher values, data for Vandana were more common in the lower-left quadrant with smaller values, and for N22 and IR64 were intermediate (Fig. 4C).

4. Discussion

4.1. Rice phenology, grain yield, canopy temperature, RH and VPD

The temperature treatments were imposed from 68 DAE, when the four genotypes were at about panicle initiation (Table 3). During the initial 6-d treatment period (68–74 DAE) under ET, maximum air temperature above the canopy was 43.7°C, but plants were exposed to lower-canopy temperatures of 37.0°C (Table 4). Takanari and IR64 attained 50% anthesis at 98 and 107 DAE, respectively, and this period corresponded with the less-sensitive earlier stages of spikelet differentiation. However, Vandana and N22 attained 50% anthesis at 85 and 90 DAE, respectively, the higher temperatures in the lower canopy corresponded with the more-sensitive later stages of spikelet differentiation (Table 5). Consequently, significant reductions in spikelet fertility (Fig. 3B) and grains plant^{-1} (Fig. 3C) were observed under ET in Vandana, the earliest genotype, which was consistent with the threshold temperature for increased spikelet sterility being 33.7°C (Jagadish et al., 2007). This explains the lower grain yield in Vandana under ET relative to AT (367 vs. 481 g m^{-2}; Fig. 3F), and as a result of its reduced grain number under ET (Fig. 3C), there was also a small compensatory increase in its maximum grain size (recorded here as maximum individual grain weight, Fig. 3D). The response in N22 was consistent with Vandana, but was smaller and not statistically significant ($P < 0.10$).

Conversely, minimum temperature was low during grain-filling in the later genotypes (Tables 4, 5). Takanari encountered 10.0°C minimum temperature from 110 to 116 DAE, which coincided with determination of maximum grain size, and maximum individual grain weight was 18.2 (Fig. 3D), which was about 10% less than that has been reported elsewhere (20.5 mg, Hasegawa et al., 2019). IR64, the latest-maturing genotype, encountered minimum temperature of 12.6 to 8.7°C throughout its grain filling. These temperatures were below the base temperature (13.5°C) for rice (Sanchez et al., 2013), rice growth and development essentially cease below the base temperature. As a result, IR64 had a lower spikelet fertility percentage (Fig. 3B), grain number (Fig. 3C) and grain yield (Fig. 3F) than other genotypes in both temperature treatments. As a result of those sink limitations, there were compensatory increases in its individual grain weight (Fig. 3D) and its root DW at maturity (Fig. 1). N22 also encountered 10°C minimum temperature from 110 to 116 DAE at the end of its grain filling period (Tables 4 and 5). Nevertheless, any grain yield consequence for N22 seems more likely to have arisen from exposure to 37.0°C maximums in its later stages of spikelet differentiation, rather than from exposure to 10°C minimum temperature late in grain filling, which was after the attainment of its maximum grain size, the last stress-sensitive development process.

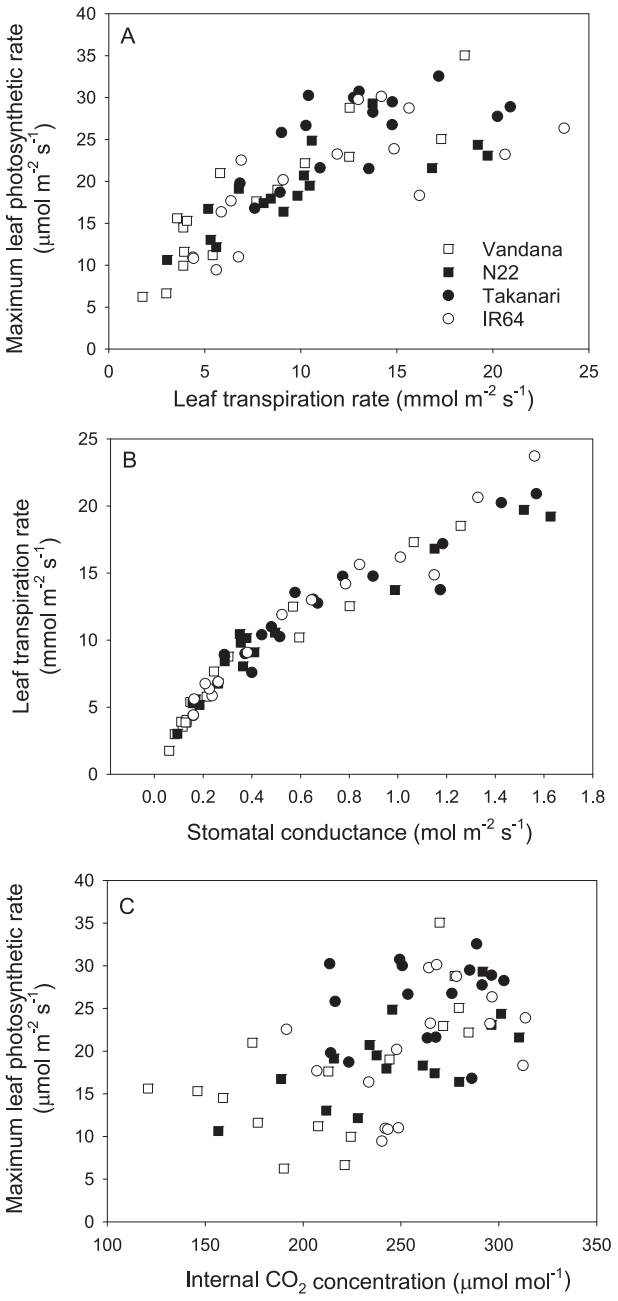

Fig. 4. The relationships between (A) maximum leaf photosynthetic rate and leaf transpiration rate, (B) leaf transpiration rate and stomatal conductance and (C) maximum leaf photosynthetic rate and leaf internal CO_2 concentration, for four rice genotypes (Vandana, N22, Takanari, IR64) grown under ambient temperature and elevated temperature treatments in large field chambers. Further details are presented in Table S4.

The rankings in sensitivity to heat tolerance here seemed at first to have little relationship with the earlier literature reports (Jagadish et al., 2008; Matsui et al., 2005; Pasuquin et al., 2013; Prasad et al., 2006; Takai et al., 2006), but this could be explained by only Vandana, and perhaps N22, which actually encountered maximum temperatures above the critical temperature of 33.7°C (Jagadish et al., 2007). The four genotypes were selected for study because of their reportedly different responses in sensitivity to high temperature during spikelet development and because of their reported genetic diversity (McNally et al., 2009). If the purpose was solely to consider the contribution of plant traits to heat tolerance, genotypes of similar phenology but differing in sensitivity would have been chosen. The differences in phenology and genetic background here were considered useful, however, as they served to emphasise the importance of the conditions actually encountered by spikelets at sensitive stages of reproductive development, as discussed in the next section.

4.2. Canopy characteristics, transpiration, VPD and canopy cooling

The results presented clearly demonstrate that maximum air temperature above the canopy decreased from above-canopy to mid-canopy and to lower-canopy with larger reductions under ET (Tables 1, 2, Fig. S1–S4, Appendix 1). This was consistent with Matsui et al. (2007, 2014), who also conducted field experiments under high VPD conditions in southern Australia, and postulated that lower temperatures in the canopy were due to higher rates of transpiration. This contention is supported here with transpiration rate consistently higher under ET for all genotypes in these high VPD conditions (Table S4, Fig. 4B).

Further, genotypes differed in the extent of canopy cooling (above-canopy minus lower-canopy, Table 2), with less overall reduction in Vandana and IR64 (4.6 and 4.3°C) than in N22 and Takanari (6.7 and 6.6°C), respectively. Interestingly, Vandana and IR64 were taller (115–130 and 90–110 cm) than N22 and Takanari (each 70–80 cm) (Table 3). For canopy cooling to be effective, however, stratification of air layers must occur within the crop canopy (Fig. S1), and this may be more effective under a shorter and denser canopy, as in N22 and Takanari. Both Vandana and N22 were exposed to maximum lower-canopy temperatures of 37.0°C during the later stages of spikelet differentiation, but the damage was greater in Vandana, an upland-adapted rice genotype (Botwright-Acuna et al., 2008), which was 5 d earlier and 50 cm taller than N22. This implied that genotypes with appropriate canopy structure should be chosen for high VPD conditions. Likewise, the greater impact of minimum temperature during grain filling may partly be due to the taller canopy in IR64 than Takanari, though IR64 also had a longer duration of exposure. Overall, this evidence supports the contention that, as well as the timing of critical stages in spikelet differentiation, the maximum canopy temperature, RH and VPD all need to be specified, in order to adequately define the critical threshold for heat tolerance of a genotype over a range of environmental conditions.

4.3. Leaf gas exchange, rice growth, grain yield and yield potential

The above discussion clearly establishes that responses were dominated by the interactions between phenology and high-temperature stress during later spikelet differentiation, and between phenology and low-temperature stress during grain filling. As a consequence, much of the complexity in trait expression can be accounted for by phenology interactions. The temperature treatments did influence a number of plant growth parameters during and after the treatment period (Fig. 1, Table S1), with their impact being clarified when adjusted for differences prior to treatment (Fig. 2, Table S2). Leaf gas exchange characteristics also differed among genotypes (Fig. 4, Table S4), with consequences for grain yield and yield components in Fig. 3 and Table S3. The response of each genotype is considered in turn below, followed by consideration of which traits may have contributed to any performance advantage.

Vandana was early maturing (Table 3), so its leaf expansion was completed before the treatment period (Fig. 2A) and its grain filling was completed before the occurrence of low minimum temperatures (Tables 4, 5). Vandana was intermediate in photosynthetic capacity (Fig. 4A), which was limited by its lower Ci (Fig. 4C). Consequently, Vandana's growth responses were predominantly due to exposure to maximum canopy temperatures of 37.0°C under ET during late reproductive stage, as modified by the reduced effectiveness of its canopy temperature stratification due to its taller stature.

Conversely, the response of IR64, the latest-flowering genotype, was dominated by exposure to low minimum temperature during grain filling. IR64 was intermediate for gas exchange characteristics (Fig. 4), and was also taller in stature (90–110 cm), though not as tall as Vandana. Consequently, exposure to lower minimum temperature during grain filling, probably exacerbated by poorer stratification of canopy temperature in the taller canopy, resulted in fewer grains being filled (Fig. 3D), and excess DW beyond grain sink capacity being allocated to roots during grain filling (Fig. 2, Table S2).

N22 was also early maturing (Table 3), but its leaf area was still expanding during the treatment period (Fig. 2A), before decreasing to a greater extent than in other genotypes under ET (Fig. 2C). Despite having the highest DW at maturity (Fig. 2F), N22 had the lowest photosynthetic capacity coupled with intermediate internal CO_2 concentration. This form of response, with greater leaf senescence and lower photosynthetic capacity, seems consistent with increased partitioning of assimilates from senescing leaves under stress, as has been reported for rice genotype NSG19 in field experiments in India (Kumar et al., 2006). This DW redistribution to stabilise grain yield under stress may partly account for the reputation of N22 as a heat-tolerant genotype, although this explanation needs further experimental evaluation.

Takanari was notable for its greater retention of leaf area in both treatments, declining by only 168 cm^2 $plant^{-1}$ overall (Fig. 2C), or by only 0.89 g $plant^{-1}$ in leaf DW (Table S2), and this was associated with higher spikelets $plant^{-1}$ and higher grains $plant^{-1}$ (Fig. 3A, C). Nevertheless, its reduced tiller number and slower DW increase (Fig. 1, Table S1) suggest that it may have benefitted from a closer plant spacing to further increase its maximum DW and spikelets $plant^{-1}$, and hence, its yield potential. The cold spell at 110–116 DAE also restricted its maximum grain size. Realising this higher potential may have increased its grain DW $plant^{-1}$ by 10–15%, or its grain yield from 512 to 588 g m^{-2}.

In leaf gas exchange characteristics, the greater photosynthetic capacity of Takanari (Fig. 4A) was related to the maintenance of a higher Ci relative to other genotypes (Fig. 4C). The combined effects of greater leaf area retention (Fig. 2), higher photosynthetic capacity (Fig. 4) and consistently higher leaf Tr (Fig. 4, Table S4), would be expected to result in a higher potential grain yield in Takanari, relative to other genotypes. Other studies have also shown Takanari to have a higher Gs under conditions of high VPD (Ohsumi et al., 2008) and higher photosynthetic capacity and grain yield (Chen et al., 2014).

Thus, in Takanari, the greater response to ET was facilitated by retention of green leaf area, higher leaf photosynthetic rate, maintenance of Ci, high spikelets $plant^{-1}$ and high grains $plant^{-1}$. This combination would seem beneficial at least when Tr can continue unabated, but even in other situations, should provide some benefit. This hypothesis requires further testing for rice under aerobic, rainfed lowland and rainfed upland conditions in the field, to see if improved canopy characteristics can have benefits over diverse environments. The characteristics noted should also provide benefits under elevated canopy temperature, so should be advantageous in future climate scenarios, as rice genotypes with greater heat tolerance will be needed in the future.

Conclusions

Field chambers were effective in raising mean above-canopy maximum daytime temperatures from 29.9°C to 41.1°C during 12 d of ET treatment (68–80 DAE), while increased Tr under ET resulted in lowering of mean lower-canopy maximum temperature to 33.2°C. Nevertheless, the earliest genotype Vandana encountered a hot spell of 37.0°C at 68–74 DAE in the lower canopy at its late reproductive stage, which exceeded the spikelet sterility threshold of 33.7°C, so its spikelet fertility, grain number and grain yield were reduced under ET. Genotypes differed in the extent of canopy cooling, with less reduction in Vandana and IR64 than in N22 and Takanari. For canopy cooling to be effective, stratification of air layers must occur within the canopy, which was more effective under the shorter and denser canopy of N22 and Takanari than under IR64 and Vandana. Genotypes with appropriate canopy structure should be chosen for high VPD conditions. Both maximum canopy temperature and VPD need to be specified to define the critical threshold for heat tolerance. Takanari was notable for greater leaf area retention and greater leaf photosynthetic capacity due to maintenance of a higher Ci, which led to higher spikelet and grain numbers and a higher yield potential under ET conditions.

Abbreviations

Amax	Light-saturated net photosynthetic rate
AT	Ambient temperature
Ci	Intercellular CO_2 concentration
DAE	Days after emergence
ET	Elevated temperature
Gs	Stomatal conductance
RH	Relative humidity
Tr	Transpiration rate
VPD	Vapour pressure deficit

Availability of data and materials

Data will be shared upon request by the readers.

Authors' contributions

Conception, E.S.P., P.L.E., T.H., and T.L.; Data collection, E.S.P. and P.L.E.; Data analysis, E.S.P., P.L.E., and D.H.; Manuscript writing, E.S.P., P.L.E., T.H., T.L., and L.J.W.; Data reanalysis, D.H. and L.J.W.; Manuscript revision, L.J.W. and E.S.P.

Declaration of Competing Interests

The authors declare that they have no competing interests. Authors Toshihiro Hasegawa, Tanguy Lafarge, and Len J. Wade (Editorial Board members) were not involved in the journal's review nor decisions related to this manuscript.

Acknowledgements

We thank AusAID for the Australian Leadership Award which allowed EMP to pursue a Ph.D. at the Charles Sturt University, Graham Centre for financial support for field chambers and experiments, Mr Kerry Schirmer for dedicated assistance and Ms. Kamala Anggamuthu for administrative support.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.crope.2023.04.004.

References

Botwright Acuna, T.L., Lafitte, H.R., Wade, L.J., 2008. Genotype × environment interactions for grain yield of upland rice backcross lines in diverse hydrologic environments. Field Crops Res. 108, 117–125.

Chen, C.P., Sakai, H., Tokida, T., Usui, Y., Nakamura, H., Hasegawa, T., 2014. Do the rich always become richer? Characterizing the leaf physiological response of the high-yielding rice cultivar takanari to free-air CO_2 enrichment. Plant Cell Physiol. 55, 381–391. https://doi.org/10.1093/pep/pcu009.

Fairhurst, T.H., Dobermann, A., 2002. Rice in the global food supply. Better Crops Intl. 16, 3–6.

Hasegawa, T., Sakai, H., Tokida, T., Usui, Y., Nakamuri, H., Wakatsuki, H., Chen, C.D., Ikawa, H., Zhang, G., Nakano, H., Matsui, T., Cima, M.Y., Hagashi, K., 2019. A high-yielding rice cultivar "takanari" shows no N constraints on CO_2 fertilization. Front. Plant Sci. 10, 361. https://doi.org/10.3389/fpls.2019.00361.

Intergovernmental Panel on Climate Change (IPCC), 2012. Summary for policymakers. In: Field, C.B., Barros, V., Stocker, T.F., Qin, D., Dokken, D.J., Ebi, K.L., Mastrandrea, M.D., Mach, K.J., Plattner, G.-K., Allen, S.K., Tignor, M., Midgley, P.M. (Eds.), Managing the Risks of Extreme Events and Disasters to Advance Climate

Change Adaptation. A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change. Cambridge Univ. Press, Cambridge, UK and New York, USA, pp. 1–19.
Intergovernmental Panel on Climate Change (IPCC), 2013. Summary for policymakers. In: Stocker, T.F., Qin, D., G-K Plattner, M., Tignor, M.B., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), Climate Change 2013 the Physical Science Basis. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge Univ. Press, Cambridge, UK and New York, USA, pp. 1–27.
Isbell, R.F., 2002. The Australian Soil Classification. CSIRO Publishing, Melbourne, Australia.
Jagadish, S.V.K., Craufurd, P.Q., Wheeler, T.R., 2007. High temperature stress and spikelet fertility in rice (*Oryza sativa* L.). J. Exp. Bot. 58, 1627–1635.
Jagadish, S.V.K., Craufurd, P.Q., Wheeler, T.R., 2008. Phenotyping parent of mapping populations of rice (*Oryza sativa* L.) for heat tolerance during anthesis. Crop Sci. 48, 1140–1146.
Jagadish, S.V.K., Mathurajan, R., Oane, R., Wheeler, T.R., Heuer, S., Bennett, J., Craufurd, P.Q., 2010. Physiological and proteomic approaches to address heat tolerance during anthesis in rice (*Oryza sativa L.*). J. Exp. Bot. 61, 143–156.
Julia, C., Dingkuhn, M., 2013. Predicting temperature induced sterility of rice spikelets requires simulation of crop-generated microclimate. Eur. J. Agron. 49, 50–60.
Krishnan, P., Balasubramanian, R., Reddy, K.R., Reddy, V.R., 2011. High temperature effects on rice growth, yield and grain quality. Adv. Agron. 111, 87–206.
Kumar, R., Sarawgi, A.K., Ramos, C., Amarante, S.T., Ismail, A.M., Wade, L.J., 2006. Partitioning of dry matter during drought stress in rainfed lowland rice. Field Crops Res. 98, 1–11.
Martinez-Eixarch, M., Ellis, R.H., 2015. Temporal sensitivities of rice seed development from spikelet fertility to viable mature seed to extreme-temperature. Crop Sci. 55, 354–364.
Matsui, T., Kobayasi, K., Kagata, H., Horie, T., 2005. Correlation between viability of pollination and length of basal dehiscence of the theca in rice under a hot-and-humid condition. Plant Prod. Sci. 8, 109–114.
Matsui, T., Kobayasi, K., Nakagawa, H., Yoshimoto, M., Hasegawa, T., Reinke, R., Angus, J., 2014. Lower-than-expected floret sterility of rice under extremely hot conditions in a flood-irrigated field in New South Wales, Australia. Plant Prod. Sci. 17, 245–252. https://doi.org/10.1626/pps.17.245.
Matsui, T., Kobayashi, K., Yoshimoto, M., Hasegawa, T., 2007. Stability of rice pollination in the field under hot and dry conditions in the Riverina region of New South Wales, Australia. Plant Prod. Sci. 10, 57–63.
Matsui, T., Omasa, K., 2002. Rice (*Oryza sativa* L.) cultivars tolerant to high temperature at flowering: anther characteristics. Ann. Bot. 89, 683–687.
Matsui, T., Omasa, K., Horie, T., 2001. The difference in sterility due to high temperatures during the flowering period among japonica-rice varieties. Plant Prod. Sci. 4, 90–93. https://doi.org/10.1626/pps.4.90.
McNally, K.L., Childs, K.L., Bohnert, R., Davidson, R.M., Zhao, K., Ulat, V.J., Zeller, G., Clark, R.M., Hoen, D.R., Bureau, T.E., Stokowski, R., Ballinger, D.G., Frazer, K.A., Cox, D.R., Padhukasahasram, B., Bustamante, C.D., Weigel, D., Mackill, D.J., Bruskiewich, R.M., Ratsch, G., Buell, C.R., Leong, H., Leach, J.E., 2009. Genomewide SNP variation reveals relationships among landraces and modern varieties of rice. Proc. Natl. Acad. Sci. U. S. A. 106, 12273–12278. https://doi.org/10.1073/pnas.0900992106.
Nagai, T., Makino, A., 2009. Differences between rice and wheat in temperature responses of photosynthesis and plant growth. Plant Cell Physiol. 50, 744–755.
Ohsumi, A., Hamaski, A., Nakagawa, H., Homma, K., Horie, T., Shiraiwa, T., 2008. Response of leaf transpiration to vapour pressure deficit in rice (*Oryza sativa* L.) varieties in relation to stomatal and leaf internal conductance. Plant Prod. Sci. 11, 184–191.
Pasuquin, E.M., Hasegawa, T., Eberbach, P., Reinke, R., Wade, L.J., Lafarge, T., 2013. Responses of eighteen rice (*Oryza sativa* L.) cultivars to temperature tested using two types of growth chambers. Plant Prod. Sci. 16, 217–225.
Prasad, P.V.V., Boote, K.J., Allen Jr., L.H., Sheehy, J.E., Thomas, M.G., 2006. Species, ecotype and cultivar differences in spikelet fertility and harvest index of rice in response to high temperature stress. Field Crops Res. 95, 398–411.
Sanchez, B., Rasmussen, A., Porter, J.R., 2013. Temperatures and the growth and development of maize and rice: a review. Global Change Biol. 20, 408–417. https://doi.org/10.1111/gcb.12389.
SAS, 2008. SAS Online 9.2. SAS Institute Inc., Cary, USA.
Steel, R.G.D., Torrie, J.H., 1960. Principles and Procedures of Statistics. McGraw Hill Book Co, New York, USA, p. 481.
Takai, T., Matsuura, S., Nishio, T., Ohsumi, A., Shiraiwa, T., Horie, T., 2006. Rice yield potential is closely related to crop growth rate during late reproductive period. Field Crops Res. 96, 328–335.
Tian, X., Matsui, T., Li, S., Yoshimoto, M., Kobayasi, K., Hasegawa, T., 2010. Heat-induced floret sterility of hybrid rice (*Oryza sativa* L.) cultivars under humid and low wind conditions in the field of Jianghan Basin, China. Plant Prod. Sci. 13, 243–251.
Wassmann, R., Jagadish, S.V.K., Heuer, S., Ismail, A., Redona, E., Serraj, R., Singh, R.K., Howell, G., Pathak, H., Sumfleth, K., 2009a. Climate change affecting rice production: the physiological basis for possible adaptation strategies. Adv. Agron. 101, 59–122.
Wassmann, R., Jagadish, S.V.K., Sumfleth, K., Pathak, H., Howell, G., Ismail, A., Serraj, R., Redona, E., Singh, R.K., Heuer, S., 2009b. Regional vulnerability of climate change impacts on Asian rice production and scope for adaptation. Adv. Agron. 102, 91–133.
Weerakoon, W.M.W., Maruyama, A., Ohba, K., 2008. Impact of humidity on temperature induced grain sterility in rice (*Oryza sativa* L.). J. Agron. Crop Sci. 194, 135–140.
Yoshida, S., 1981. Fundamentals of Rice Crop Science. International Rice Research Institute, Los Baños, the Philippines.
Zwiers, F.W., Zhang, X., Feng, Y., 2011. Anthropogenic influence on long return period daily temperature extremes at regional scales. J. Clim. 24, 881–892. https://doi.org/10.1175/2010JCLI3908.1.