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Me a-anal i and do e-re pon e anal i of high empera re effec on rice ield and q ali

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A R T I C L E I N F O

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A B S T R A C T

Global arming i one of he bigge challenge for impro ing he prod c i i of rice crop in he f re. In hi d , a me a-anal i and a do e-re pon e anal i ere cond c ed i h da a collec ed from 95 p blica ion o d he differen ial re pon e of ph iological rai , ield componen , and grain q ali o high da and nigh empera re in rice. O erall, grain ield a red ced b 39.6% (i h 95% CI from −42.9% o −35.6%) nder high empera re, hich a primaril ca ed b he decrea e of eed e percen age. Yield red c ion ca ed b high empera re ere a ocia ed i h a decrea e in pho o n he i and an increa e in re pira ion. High empera re affec ed grain q ali b decrea ing head rice percen age and increa ing chalk rice ra e and chalkine . The red c ion of grain ield nder high da empera re a primaril ca ed b he red c ion in eed e percen age. Ho e er, nder high nigh empera re, he combina ion of decrea ed pikele n mber per panicle, grain eigh , and bioma prod c ion in addi ion o decrea ed eed e percen age con rib ed o he decline of grain ield . The e re l gge ha he differen ial effec of da and nigh arming on he proce e ha con rib e o forma ion of rice ield ho ld be con idered hen ne rice c l i ar are de eloped a a crop adap a ion ra eg for f re global arming.

1. Introduction

Clima e change repre en an con in al challenge for agric l ral prod c ion and food ec ri (IPCC in Core Wri ing Team, 2014). Global arming i an impor an a pec of clima ic change ha i largel dri en b increa ing a mo pheric concen ra ion of greenho e ga e , ra o pheric o one deple ion, aero ol emi ion and land- e change (Schneider, 2001; Shak n e al., 2012). The freq enc and in en i of e reme ea her e en ch a regional dro gh and hea a e are predic ed o increa e i h global arming (Dale e al., 2001). Mo clima e model predic ha he global empera re ill increa e from 0.3 o 6.4 C a he end of hi cen r depending on he mi iga ion of a mo pheric greenho e ga emi ion (IPCC in Core Wri ing Team, 2014; Meehl e al., 2007). S ch an increa e in air empera re ill profo ndl affec crop prod c ion (Lobell and A ner, 2003), and man die ho a ignifican infl ence of ele a ed empera re on crop ield. According o Lobell and A ner (2003), bo h corn and o bean ield ill decrea e appro ima el 17% for each degree increa e in air empera re in he USA. Coinciden all , Peng e al. (2004) fo nd ha a 1.13 C increa e in nigh empera re o er a period of 25 ear (1979–2003) markedl decrea ed rice grain ield in he Philippine .

Rice (*Oryza sativa* L.) i prod ced nder a ide range of clima ic condi ion and i a aple food crop for more han 50% of he orld' pop la ion (Maclean e al., 2002). Hence, he re pon e of rice o high empera re m be de ermined o de elop adap a ion ra egie o achie e ainable crop prod c ion o mee he demand of a gro ing pop la ion (Ho den e al., 2007). Pre io die ho ha he gro h re pon e of rice o high empera re arie i h geno pe (Jagadi h e al., 2010a, 2007; Mar ama e al., 2013 Zi ka and Ordone , 1996). Moreo er, he reprod c i e age i likel more en i i e o high empera re re han he ege a i e age in rice (Sa nche e al., 2014; Welch e al., 2010). When empera re e ceed cri ical hre hold , an her dehi cence, pollen germina ion on he igma, and/or pollen be gro h are affec ed, and con eq en l , pikele erili increa e drama icall (lo er eed e percen age), hich re l in a erio lo of grain ield (Jagadi h e al., 2010a,b, 2007, 2011; Pra ad e al., 2006; Sa ake and Yo hida, 1978).

A mme ric arming, i h a grea er increa e in nigh han in da empera re , ha been ob er ed (Dona and Ale ander, 2012) and ome a en ion foc ed on b eq en con eq ence for ecolog and agric l re (Peng e al., 2013). Bo h high da and nigh empera re affec gro h, de elopmen , and ield forma ion of crop pecie

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(Kri hnan e al., 2011). S die repor ha high da and nigh em- pera re nega i el affec rice bioma prod c ion and grain ield (Cooper e al., 2008; Kri hnan e al., 2011; Mohammed and Tarple , 2009; Rang e al., 2011). High da empera re e erel affec rice reprod c i e proce e (I o e al., 2009; Jagadi h e al., 2007, 2010b; Madan e al., 2012; Rang e al., 2011), par ic larl pikele fer ili , herea high nigh empera re lead o an increa e in dark re pira ion and con eq en red c ion in bioma prod c ion and grain ield (Coa e al., 2015; Peng e al., 2004; Shi e al., 2013, 2016). Ho e er, o her die ho ha increa ed pikele erili i he primar rea on for ield lo nder high nigh empera re (Mohammed and Tarple , 2009, 2011). Hence, he general pa ern of empera re re pon e and he differen ial effec of high da and nigh empera re on rice ield and ield a rib e m be de ermined.

Grain q ali i an impor an cri erion for accep ance of an arie b farmer and con mer . Rice i con med primaril a an in ac kernel, and a high propor ion of broken rice lead o a red c ion in marke price from 40% o 50% (Cooper e al., 2008; Sreeni a l e al., 2015). Chalkine re l from he abnormal forma ion of arch gran- le , hich l ima el affec arch acc m la ion d ring he earl grain filling age, and he e proce e are en i i e o high empera re (Fi gerald and Re rreccion, 2009; Madan e al., 2012; Sreeni a l e al., 2015). Increa ed chalk rice ra e and decrea ed head rice per- cen age are common o come of high empera re re d ring he ripening pha e of rice crop (Kri hnan e al., 2011). Addi ionall , high empera re d ring he grain filling period ca e a ignifican red c ion in grain i e and am lo e con en (Yamaka a and Haka a, 2010; Yamaka a e al., 2007).

Man die ha e in e iga ed he po en ial effec of high em- pera re on ph iological rai , ield componen and grain q ali in rice. The e die pro ide a large da aba e for e al a ing he general re pon e of rice crop o high empera re ing a me a-anal i . Thi approach ha been ed o d he o erall re pon e of rice o ele a ed CO_2 and O_3 (Ain or h, 2008) and ha al o been cce f ll ed o mmari e crop re pon e o ele a ed CO_2 in free-air CO_2 enrichmen (FACE) e perimen (Ain or h e al., 2002). Ho e er, he general re pon e of rice o high empera re ha no been q an i a i el a - e ed o da e ing a me a-anal i , hich migh be d e o he dif- feren die ing differen high empera re rea men me hod in erm of he in en i , iming, and d ra ion. Therefore, in hi d , e ed bo h me a-anal i and do e-re pon e anal i o mmari e he effec of high da and nigh empera re on rice ph iological pro- ce e , grain ield , ield componen , and grain q ali . More peci- ficall , he goal a o an er he follo ing q e ion : (i) Wha are he re pon e of rice ph iological proce e , grain ield , ield compo- nen and grain q ali o ele a ed empera re ? (ii) Do ele a ed da and nigh empera re ha e differen effec on grain ield and ield a rib e in rice crop ?

2. Materials and methods

2.1. Data collection

The PRISMA flo diagram (Fig. S1) ho he proced re ed for he elec ion of re earch paper for hi d . Re earch paper ere earched from he Web of Science, Scop , and he China Kno ledge Re o rce In egra ed Da aba e ing fo r earch erm : 'Rice AND ele- a ed empera re', 'Rice AND high empera re', 'Rice AND increa ed empera re', and 'Rice AND arming' in December 2015. An ini ial earch re l ed in 29,428 ar icle (o al re l from he hree da a- ba e), hich ere red ced o 4264 b limi ing re earch o agric l re, plan cience, ecolog , and en ironmen al cience. Af er d plica e die ere remo ed b comparing he ar icle i le , a hor li , p blica ion ear , and jo rnal name , he ar icle n mber a red ced o 1307 record . Then, he ab rac ere e amined o j dge heir re- le ance, and 262 ar icle ere con idered rele an . The f ll e of he 262 ar icle a checked o de ermine he i abili for me a-anal i ba ed on he follo ing cri eria: (i) a lea o empera re (con rol and high) rea men ; (ii) for grain ield (GY) and ield componen (pa- nicle n mber, PN; pikele n mber per panicle, SN; eed e percen age, SPP; grain eigh , GW; and bioma , BM), onl he die ha con- ained informa ion on rea men mean , ample i e, and da a aria- bili [andard de ia ion (SD) or andard error of he mean (SE)] ere incl ded; (iii) for grain q ali rai , he die i ho informa ion on da a ariabili ere al o incl ded, beca e fe die ere a ailable on he empera re re pon e of rice grain q ali rai in he li era re; (i) ild- pe pheno pe ere elec ed and m an ere e cl ded; and ( ) o her rea men (i.e., CO_2 and dro gh) ere e - cl ded. The die elec ed for do e–re pon e anal i me he fol- lo ing cri eria: (i) for ph iological rai (ligh - a ra ed pho o n h- e i and re pira ion), he gro h empera re and mea remen empera re ere repor ed, i h a lea o mea remen empera- re ; (ii) for grain ield (GY) and ield componen , a lea o empera re rea men ; and (iii) m an and o her rea men ere e cl ded. A a re l , 95 peer-re ie ed ar icle ere incl ded for bo h me a- and do e-re pon e anal e (Appendi S1).

Grain q ali parame er referred o gel con i enc , pro ein con- en , am lo e con en , chalkine , chalk rice ra e, grain leng h, grain id h, bro n rice percen age, milled rice percen age, and head rice percen age. Chalk rice ra e i defined a a ra io of grain i h opaq e par in he endo perm o o al n mber of grain , herea chalkine i defined a he percen age of chalk area o projec ed grain area (Li le e al., 2000).

The da a ere e rac ed direc l from he able and e in he original paper or indirec l from fig re ing WinDIG 2.5 (h p:// . nige.ch/ cience /chifi/cpb/ indig.h ml). When he ariance ere repor ed a SE , he ere hen con er ed in o o al ariance ing he n mber of replica e of each ola ile collec ion, mmed, and finall con er ed o SD for gro ped ola ile . O her informa ion, hen a ailable, ch a e perimen al d ra ion, c l i ar name, pe of high empera re rea men (da , nigh or hole da), gro ing condi ion (po or field), and eco pe of he geno pe , a al o e rac ed for f r her anal i .

2.2. Meta-analysis

A me a-anal i a performed ing R 3.2.2 (h p ://cran.r- projec .org). The me a-anal i con i ed of o primar ep : (1) calc la e indi id al effec i e and heir a ocia ed ariance for each d o place he da a from he primar die on a common cale, and (2) a e he acc m la i e effec i e. In he c rren d , he indi id al effec i e of rice rai ere calc la ed ing a na ral log- ran formed re pon e ra io ($\ln R = \ln\frac{X_e}{X_c}$), here X_e and X_c are he mean al e of all compari on in he con rol and high empera re rea - men , re pec i el . The random-effec model anal i , hich a ba ed on he a mp ion of random aria ion in re pon e among - die , and a eigh ed parame ric anal i ere ed for grain ield and componen . In he eigh ed anal i , he ariance of lnR (υ) a ap- pro ima ed ing he follo ing form la: $\upsilon = \frac{(SD_c)^2}{N_cX_c} + \frac{(SD_e)^2}{N_eX_e}$

here SD_c and SD_e are he andard de ia ion for all compari on in he con rol and high empera re rea men , re pec i el ; N_c and N_e are he ample i e for he con rol and high empera re rea men , re pec i el . For each d , he eigh ing fac or a calc la ed a he in er e of he pooled ariance (1/υ). The final eigh (w^*) ed in he anal e a : $w^* =$ /N, here N i he n mber of ob er a ion from he ame d . To q an if he acc m la i e effec , he eigh ed mean re pon e ra io $\left(\text{Ln}RR = \sum_{i=1}^{k} w_i^* R_i / \sum_{i=1}^{k} w_i^*\right)$ and i 95% CI ere cal- c la ed b he reciprocal of he mi ed-model ariance (C r i and Wang, 1998; an Groenigen e al., 2011). An n eigh ed anal i a cond c ed for grain q ali parame er for hich a lack of informa ion on da a ariance allo ed onl a re- ampling calc la ion (McGra h and Lobell, 2013; Morgan e al., 2003). Re pon e effec ere e ima ed a a percen age change rela i e o he con rol (%), ing he eq a ion A = ($e^{\ln RR}$ − 1 100%). When he 95% CI did no o erlap i h ero, he empera re effec ere con idered a i icall ignifican .

Be ond e ing he her he acc m la i e effec i e for each gro p are ignifican l differen from ero, he her he gro p differed from one ano her i al o of in ere (He erogenei). In he c rren d , a homogenei e a applied in hich o al he erogenei (Q_T) a par i ioned in o i hin-gro p (Q) and be een-gro p (Q_b) he ero- genei ie . The e par i ion ere calc la ed a :

$$Q_b = \sum_{j=1}^{m} \sum_{i=1}^{k_j} w_{ij} (\ln RR_j - \ln RR)^2$$

$$= \sum_{=} \sum_{=} \quad -$$

Table 1
The empera re range and mean of hree high empera re pe incl ded in *meta*-anal i .

HT pe	No.	CK range (C)	CK mean (C)	HT range (C)	HT mean (C)	ΔT range (C)	ΔT mean (C)
Da	407	21–39	28.5	24–44	34.7	1–15	6.1
Nigh	882	18–28	22.9	24–35	28.0	2–12	5.1
Whole	246	19–35	27.2	28–41	32.5	1–12	5.3
All	1535	18–39	25.1	24–44	30.5	1–15	5.4

Da , high da empera re; Nigh , high nigh empera re; Whole, high da and high nigh empera re; CK, con rol check; HT, high empera re; ΔT, he difference be een HT and CK; CK range, he empera re range of all con rol check incl ded in me a-anal i ; CK mean, he mean empera re of all con rol check incl ded in me a-anal i ; and No., he n mber of da a poin incl ded in me a-anal i . The hole da empera re a calc la ed a he a erage of da and nigh empera re for each d .

Table 2
Be een-gro p he erogenei (Q_B) for high empera re effec i e acro differen ca-egorical ariable .

Variable	No.	HT pe	Gro h condi ion	Eco pe	Geno pe	Trea age
Yield	232	35.19***	109.5***	8.49*	331.0***	19.93***
PN	161	0.91	3.87*	1.27	47.21	0.67
SN	161	9.70**	0.06	18.80***	75.58***	3.95
SSP	211	35.88***	74.62***	1.30	300.4***	43.37***
GW	124	3.31	7.86**	2.58	20.17	0.01
BM	112	12.98**	0.41	4.79	18.12	7.87*

HT, high empera re; GY, grain ield; PN, panicle n mber; SN, pikele n mber per panicle; SSP, eed e percen age; GW, grain eigh ; BM, bioma ; and No., da a poin incl ded. HT pe incl ded da , nigh , and hole da high empera re rea men ; Gro h condi ion incl ded field and po condi ion ; Eco pe incl ded *indica* and *japonica*; and Trea men age incl ded high empera re rea men before heading, af er heading, and en ire gro h ea on.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

3.1. Effects of high temperatures on rice physiological traits

Generall , ligh - a ra ed leaf pho o n he ic ra e increa ed i h empera re before he op imal empera re and decrea ed i h empera re af er op imal empera re (Fig. 1A). O erall, he op im m empera re for rice pho o n he i a appro ima el 30 C. Ho e er, he op im m empera re for pho o n he i aried i h gro h empera re (Fig. 1C). Plan gro n a lo empera re ho ed grea er pho o n he ic capaci a lo er empera re , herea plan gro n a high empera re ho ed grea er capaci for pho o n he i a higher empera re . We al o fo nd ha leaf re pira ion ra e increa ed ignifican l i h high empera re (Fig. 1B and D). The re pira ion increa ed i h empera re e ponen iall . Unlike pho o n he i , he re pon e of re pira ion o empera re a independen from gro h empera re (Fig. 1D).

3.2. Effects of high temperatures on rice yield attributes

O erall, high empera re ignifican l red ced rice grain ield (-39.6%, i h a 95% CI of −42.9% o −35.6%) and eed e percen age

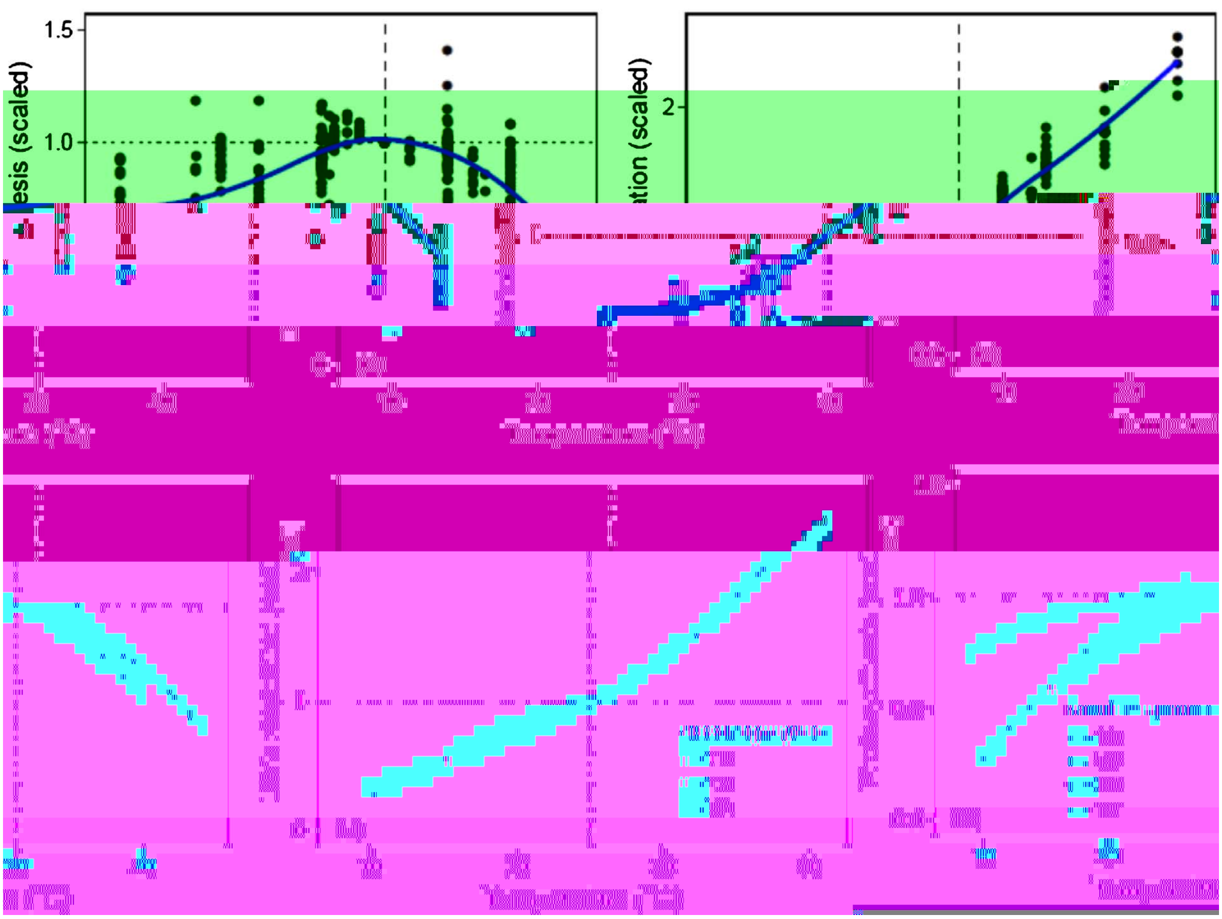

Fig. 1. Effec of high empera re on rice ph iological rai . General re pon e of ligh - a ra ed pho o n he i (A) and dark re pira ion (B) o mea ring empera re, and he gro h empera re depended re pon e of ligh - a ra ed pho o n he i (C) and dark re pira ion (D) o mea ring empera re. To demon ra e he re pon e of ph iological rai o empera re nder differen gro h empera re more clearl , he da a poin in (C) and (D) ere no ho n. The reference al e for empera re i indica ed b do ed line (30 C for pho o n he i and 25 C for re pira ion).

(−33.3%, i h a 95% CI of −36.9% o −29.5%) (Fig. S2). Ho e er, he effec of high empera re on panicle n mber (−0.69%, i h a 95% CI of −7.54% o 6.67%), pikele n mber per panicle (−6.83%, i h a 95% CI of −13.30% o 0.09%), grain eigh (−4.92%, i h a 95% CI of −12.36% o 3.15%) and bioma (8.07%, i h a 95% CI of −0.91% o 17.86%) a no ignifican .

Significan difference in empera re re pon e ere ob er ed among he hree pe of high empera re rea men for grain ield (Q_b = 35.19, $P < 0.001$), pikele n mber per panicle (Q_b = 9.70, $P < 0.05$), eed e percen age (Q_b = 35.88, $P < 0.001$), and bioma (Q_b = 12.98, $P < 0.01$) (Table 2). Ho e er, empera re re pon e in panicle n mber (Q_b = 0.91, P = 0.738) and grain eigh (Q_b = 3.31, P = 0.184) ere no ignifican l differen among he pe of high empera re rea men . Dra ic red c ion in grain ield and eed e percen age occ rred in he high da (−56.3% and −53.4%, re pec i el), nigh (−31.9% and −18.0%, re pec i el), and hole da (−68.3% and −35.4%, re pec i el) empera re rea men (Fig. 2). Bioma decrea ed nder high nigh empera re, herea an oppo i e re pon e a ob er ed nder high hole da empera re and no re pon e nder high da empera re. Spikele n mber per panicle and grain eigh decrea ed onl nder high nigh empera re b no nder high da and hole da empera re . Moreo er, panicle n mber did no re pond o an of he high empera re rea men . To be er nder and he re pon e pa ern of grain ield and i componen o high empera re, e anal ed heir do e-re pon e c r e o da empera re (Fig. 3) and nigh empera re (Fig. 4). O r re l ho ha he op im m da empera re for rice grain ield a appro ima el 28 C. When he empera re ere lo er han he op imal da empera re, grain ield a increa ed i h da empera re b increa ing bioma and pikele n mber per panicle, hile he panicle n mber decrea ed i h da empera re. When he empera re ere higher han op imal da empera re, he decrea e in grain ield 7.97020388-404.9(-46

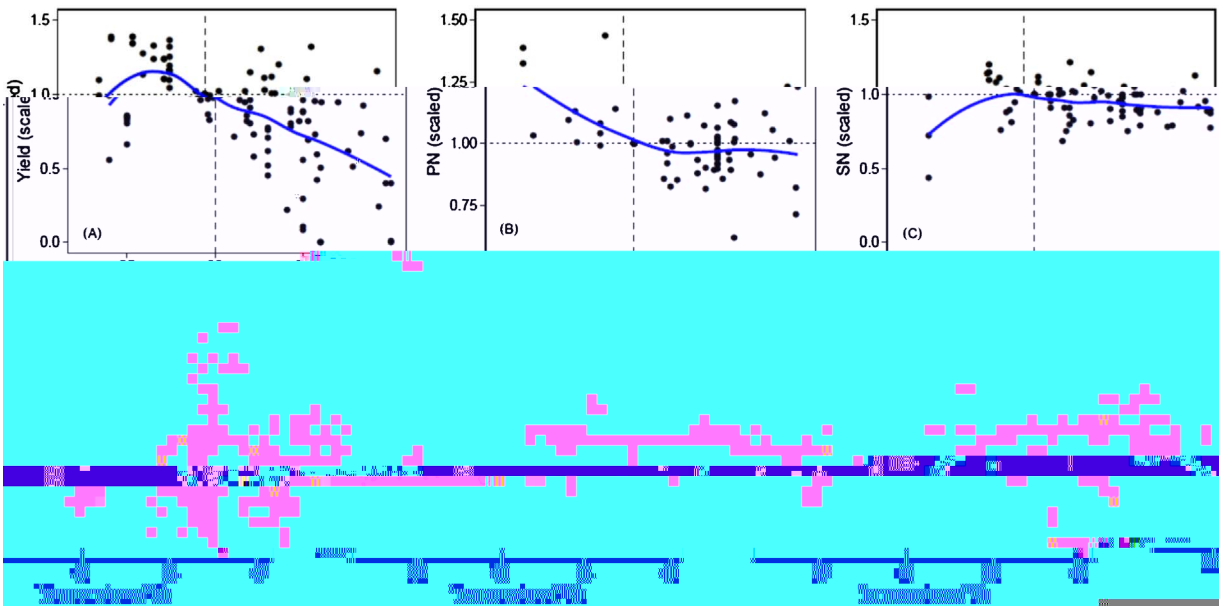

Fig. 3. Do e-re pon e anal i of high da empera re effec on rice ield a rib e . General re pon e of (A) grain ield (GY), (B) panicle n mber (PN), (C) pikele n mber per panicle (SN), (D) eed e percen age (SSP), (E) grain eigh (GW), and (F) bioma (BM) o high da empera re. The reference al e for empera re i indica ed b do ed line (30 C).

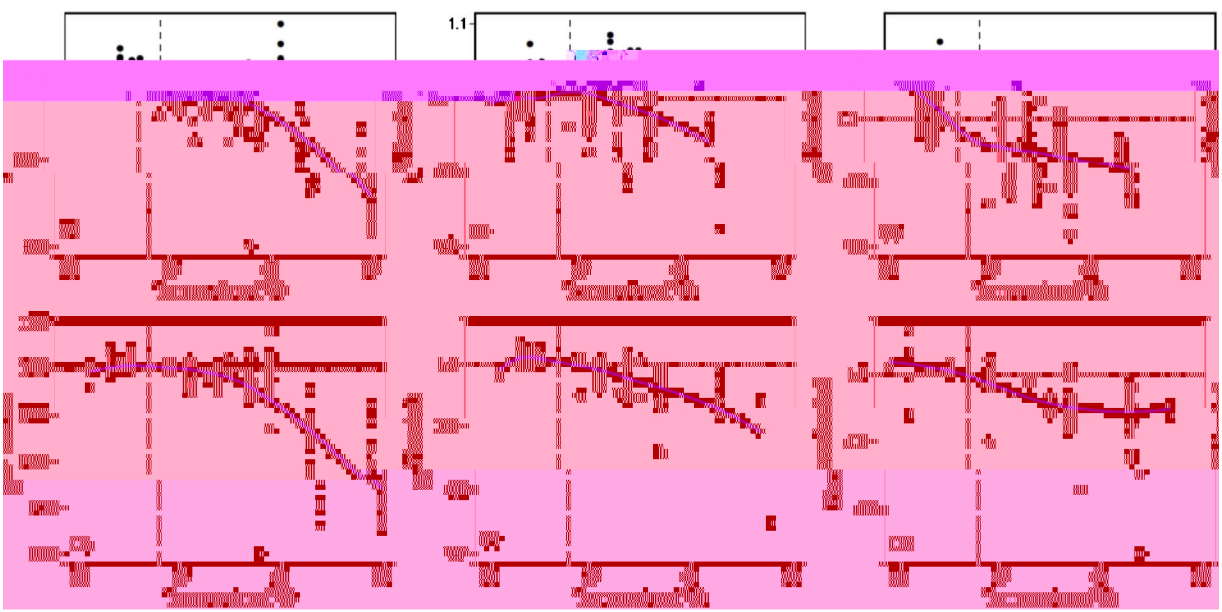

Fig. 4. Do e-re pon e anal i of high nigh empera re effec on rice ield a rib e . General re pon e of (A) grain ield (GY), (B) panicle n mber (PN), (C) pikele n mber per panicle (SN), (D) eed e percen age (SSP), (E) grain eigh (GW), and (F) bioma (BM) o high nigh empera re. The reference al e for empera re i indica ed b do ed line (24 C).

en i i i of eq ipmen ere nlikel o ha e a rong effec on hi d (Fig. S9).

4. Discussion

4.1. Photosynthesis and respiration are responsible for decreased biomass and grain yields under high temperatures

Similar o mo C_3 plan , rice leaf ligh - a ra ed pho o n he i increa e from a ba e empera re o a lo er op im m and hen decline i h increa ing empera re from an pper op im m. O erall, he op im m empera re for pho o n he i a appro ima el 30 C in rice. Ho e er, he op im m empera re co ld be hif ed b he gro h empera re: plan gro n nder rela i el lo empera re ho ed grea er pho o n he ic capaci nder lo er empera re , hich re l ed in a lo er op im m empera re, herea plan gro n nder rela i el high empera re ho ed grea er capaci for pho o n he i nder higher empera re , hich re l ed in a higher op im m empera re. An increa e in he capaci of pho o n he ic en me ch a R bi co i likel for pho o n he ic acclima ion o lo empera re , herea pho o n he ic acclima ion o high empera re ma in ol e an increa e in he hea abili of he pho o n he ic appara (Sage and K bien, 2007; Yamori e al., 2014, 2010). Here, e fo nd ha he do e-re pon e c r e of pho o n he i o empera re a incon i en i h he do e-re pon e c r e of bioma o da empera re ; h , he decrea e in bioma nder high da empera re migh be primaril ca ed b he decline in pho o n he i . Moreo er, bioma co ld decline beca e of an increa e in pho ore pira ion nder high empera re ; ho e er, pho ore pira ion da a are limi ed d e o he echnical limi a ion in i mea remen . Dark re pira ion i con idered he primar fac or ha affec rice bioma and ield nder high nigh empera re (Peng e al., 2004). Ba ed on o r re l , dark

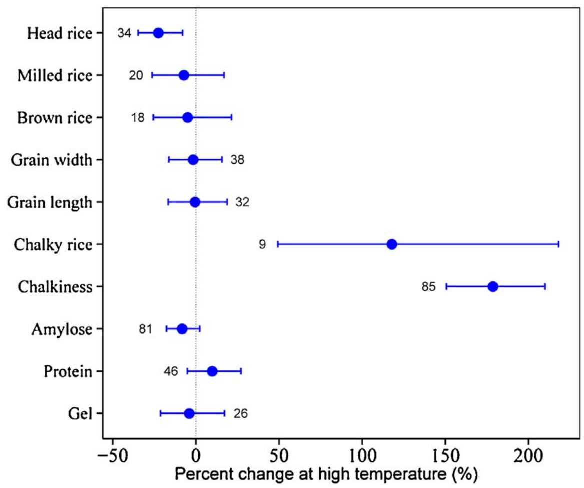

Fig. 5. Effec of high empera re on rice grain q ali ie . Error bar repre en 95% confidence in er al . The al e near he error bar indica e he n mber of da a poin for me a-anal i .

re pira ion increa ed dra icall i h increa ed empera re (Fig. 1), hich e plained he decrea e of bioma nder high nigh empera- re . Me a-anal i indica ed ha bioma increa ed ignifican l nder high hole da empera re (Fig. 2C), beca e he high em- pera re increa ed bioma prod c ion b e eral-fold hen con rol empera re ere lo er han 21 C (Fig. S10). Addi ionall , do e-re- pon e anal i gge ed ha he increa ed empera re migh con- rib e po i i el o bioma hen con rol da empera re ere lo er han 30 C (Fig. 3F).

4.2. Effects of high temperatures on yield and its components

Rice ield i compo ed of panicle n mber, pikele n mber per panicle, eed e percen age, and grain eigh . In he c rren d , e fo nd ha grain ield ere red ced ignifican l (−39.6%) nder high empera re (Fig. S2), i h he red c ion primaril ca ed b a decrea e in eed e percen age (−33.3%). Addi ionall , pikele n mber per panicle and grain eigh decrea ed ligh l b no ig- nifican l nder high empera re . The e re l gge ed ha re- prod c i e proce e and organ are more en i i e o high empera- re han ege a i e gro h. In fac , a ignifican effec of high empera re af er he heading age a de ec ed on eed e percen- age, b no for he high empera re before he heading age (Fig. S5). The decrea e in eed e percen age ind ced b high empera re a mo likel he re l of he effec of empera re re on meio i and gro h of he o arie d ring he pre-an he i period, in addi ion o empera re effec on an her dehi cence and prod c ion, ran fer, iabili , and germina ion of pollen d ring an he i (I o e al., 2009; Jagadi h e al., 2007, 2010b; Madan e al., 2012; Rang e al., 2011).

O r anal i al o ho ed ha he re pon e of grain ield and eed e percen age o high empera re differed ignifican l i h geno- pe and gro h condi ion (Table 2). The geno pe-dependen re- pon e of eed e percen age o high empera re i ob er ed in man die (Jagadi h e al., 2010a, 2007; Mar ama e al., 2013 Zi ka and Ordone , 1996). The difference in high empera re olerance among geno pe migh be ca ed b e eral mechani m . Fir , geno pic difference occ r in pollina ion abili , charac eri ed b rai ch a pollen n mber, an her i e and hape, and an her dehi cence (Jagadi h e al., 2007; Madan e al., 2012). For e ample, Mar ama e al. (2013) fo nd ha geno pe i h large an her and more ab ndan pollen had be er pollina ion abili ie nder high empera re . Second, he hermal condi ion of he pikele ca ed b ran pira ion abili co ld be differen acro geno pe (Xiong e al., 2015). Finall , he iming of flo ering can be differen among geno pe . For e ample, geno pe i h an earl -morning flo ering rai had le erili d e o he cooler morning air han a midda (I himar e al., 2010). In he pre en d , e fo nd ha he red c ion of ield in po a more erio han ha in he field (Fig. S3). Me hodologicall , crea ing a large empera re gradien nder field condi ion i more diffic l han for po in he labora or and greenho e. Moreo er, e reme high em- pera re ere reached in fe field die . Addi ionall , o her en- ironmen al fac or are al o diffic l o con rol in he field, ch a air h midi , and he in erac ion be een high empera re and o her en ironmen al fac or nder field condi ion ma con rib e o hi difference. Recen die gge ha more open-field die are re- q ired o confirm he empera re re pon e (J lia and Dingk hn, 2012; Ma i e al., 2014).

O erall, grain ield decrea ed nder bo h high da and nigh empera re . Thi re l i in con ra o ho e repor ed b Welch e al. (2010) ho ho ed ha farm field rice ield decrea ed i h high dail minim m empera re b increa ed i h high dail ma im m em- pera re. The dail ma im m empera re of differen i e and ear in heir d ere . er clo e o 30 C; ho e er, he ma im m da empera re in he c rren d i higher han 40 C (Table 1; Fig. 3). In fac , o r re l al o ho ed ha a da empera re of appro ima el 28 C had a po i i e effec on rice ield (Fig. 3A).

In hi d , e ob er ed he differen ial effec of high da and nigh empera re on rice ield forma ion. The red c ion of grain ield nder high da empera re a primaril ca ed b he red c ion in eed e percen age. Ho e er, decrea ed pikele n mber per panicle, grain eigh , and bioma prod c ion in addi ion o decrea ed eed e percen age con rib ed collec i el o he decline of grain ield nder high nigh empera re (Fig . 2–4Fig re 2). The decrea e in pikele n mber per panicle and grain eigh , hich de ermine he ink capa- ci , migh be ca ed b he decline in a imila ion ppl d e o he increa e in re pira ion nder high nigh empera re . In fac , pikele are le compe i i e han he em for a ailable a imila e d ring pa- nicle forma ion in hea (Fi cher and S ockman, 1980). D ring grain filling, carboh dra e are from ei her c rren pho o n he i direc l or ran loca ed from a imila e acc m la ed in he leaf hea h and c lm before heading. Red ced grain eigh nder high nigh empera re ma be a re l of he carboh dra e ppl failing o mee he demand of an accelera ed ra e of grain filling (Shi e al., 2013).

The finding of differen ial effec of high da and nigh empera- re on rice ield forma ion i no el. Ho e er, ch a concl ion co ld be confo nded i h differen rea men me hod be een da and nigh in erm of he in en i , iming, and d ra ion of high empera re rea men . In addi ion o he me a-anal i , he do e-re pon e anal i al o confirmed ha high da and nigh empera re had differen ef- fec on ield componen . Therefore, he in en i of high empera re rea men ho ld no be a confo nding fac or for he differen ial ef- fec of high da and nigh empera re on rice ield forma ion. F r hermore, he iming and d ra ion of high empera re rea men ere randoml ariable acro all die (Table S3); h , high da and nigh empera re rea men did no ho con i en difference in iming and d ra ion of he rea men . We al o checked he iming of high empera re rea men for he ob er a ion of panicle n mber and pikele n mber per panicle in he me a-anal i (Fig. 2) and fo nd ha all ob er a ion for bo h da and nigh recei ed high empera re rea men before he heading age (da a no ho n).I i ell kno n ha reac i e o gen pecie (ROS) can be genera ed nder re con- di ion incl ding high empera re and plan cell (e.g. membrane) inj red b acc m la ed ROS (A ada, 2006). Recen l , Lai e al. (2012) fo nd ha ROS-re pon e gene e hibi a ime-of-da - pecific pha e of e pre ion nder di rnal and circadian condi ion , and he efficienc of ROS ca enging em i high d ring he da . B eon and Back (2014) ob er ed ha more de rimen al effec of high nigh empera re han high da empera re in rice i ell correla ed i h he prod c ion of mela onin − ac ing a a po en an io idan hich can efficien l ca- enge ROS in he plan cell − nder high nigh empera re.

Therefore, he le efficienc of ROS ca enging em d ring he nigh i likel one of he rea on ha rice prod c ion i more en i i e o ele a ed nigh empera re. In addi ion, n he i and acc m la ion of hea hock pro ein (HSP) and cold hock pro ein (CSP) al o gge ed pla ing an impor an in hea olerance, ho e er, mechani m are ill no cer ain (Gro er e al., 2013; King and Macrae, 2015). F r her die ill be nece ar o re eal he mechani m of rice ield re pon e o a mme ric arming.

4.3. High temperature effects on grain quality

Among grain q ali rai , chalkine , chalk rice ra e, and head rice percen age ho ed ignifican re pon e o high empera re rea men , herea he effec of high empera re on o her grain q ali rai ere no ignifican . High empera re increa ed chalkine and chalk rice ra e b red ced head rice percen age. The effec of high empera re rea men on chalkine a grea er nder high hole da empera re han nder high da and nigh empera re alone. Chalkine i one of he ke fac or in de ermining rice q ali and commercial price and de rac from grain appearance and herefore decrea e marke accep ance. Head rice percen age i a deci i e fac or for mea ring milled rice q ali . Pre io die repor ha grain q ali rai ch a chalkine and head rice percen age are er en i i e o high empera re (Cooper e al., 2008; Fi gerald and Re rreccion, 2009; Madan e al., 2012; Sreeni a l e al., 2015). The high empera re re d ring he filling age rigger non- niform filling and impairmen in orage bio n he i , hich lead o chalk forma ion. The gap formed d e o abor ed arch gran le forma ion are ho gh o be re pon ible for making chalk grain more bri le and for forming fi re along he grain (Sreeni a l e al., 2015). A a re l , chalk grain crack ea il d ring grain proce ing, hich declined head rice percen age a a con eq ence of he increa ed amo n of broken grain (Sreeni a l e al., 2015).

5. Conclusions

To iden if , elec , and breed i able c l i ar for a arming orld, nder anding he effec of high empera re on rice ield forma ion i an rgen a k. Here, e ho ed ha high empera re profo ndl infl enced rice ph iolog , grain ield and grain q ali . The proce e of rice ield forma ion ere affec ed differen l b high da and nigh empera re . The red c ion of ield nder high da empera re a primaril ca ed b a decrea e in eed e percen age; ho e er, decrea ed pikele n mber per panicle, eed e percen age, grain eigh and bioma prod c ion combined con rib ed o he decline of ield nder high nigh empera re . O r re l gge ha adap a ion ra egie in crop breeding for global arming ho ld con ider a mme ric arming and ha f r her die are req ired o nder and he difference in he ph iological mechani m nderl ing rice ield decline nder high da and nigh empera re .

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Appendix A. Supplementary data

S pplemen ar da a a ocia ed i h hi ar icle can be fo nd, in he online er ion, a h p://d .doi.org/10.1016/j.en e pbo .2017.06.007.

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