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RESEARCH ARTICLE

Varietal diversity of Sri Lankan traditional rice based on sensitivity to temperature and photoperiod at vegetative stage

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Abstract: Photoperiod and temperature are two important environmental factors affecting vegetative growth and yield of rice. The varietal diversity based on the response to temperature and photoperiod during vegetative growth was determined in a core collection of 40 Sri Lankan traditional rice accessions (SLTRA) and 2 improved and 2 wild rice types in terms of days to fully expansion of fifth leaf (DFL) and plant height (PH). Short day (SD), day neutral (DN) and long day (LD) conditions were imposed during 2 trials of high temperature (HT) and low temperature (LT) at 36.9 ± 0.43 °C and 34.0 ± 0.98 °C under natural temperature fluctuation. Average DFL of the collection at HT was significantly lower than that of the LT irrespective of photoperiods. Temperature affected the DFL of 22 accessions, while photoperiod alone affected 1 accession. Average PHs under HT were similar irrespective of the photoperiod, which were lower than those of LT. PH of 15 accessions was not affected by photoperiod or temperature. Temperature alone affected 12 accessions and photoperiod alone affected 2 accessions. Both photoperiod and temperature affected 4 accessions. In the cluster analysis on response to photoperiod and temperature, SLTRA and improved rice were differentiated into 2 clusters at a rescaled distance of 25. Further, sub-clusters grouped several accessions of the same variety together. The differential varietal response to photoperiod and temperature in SLTRA would be useful in breeding for climate change adaptations after further experiments on flowering time and yield.

Keywords: Fifth leaf stage, *Oryza sativa*, photoperiod sensitivity, temperature, traditional rice.

INTRODUCTION

Extreme climatic events create adverse impacts on ecosystems affecting global crop production. Sri Lanka is an island, which has diverse climatic zones (National Atlas of Sri Lanka, 1988; Karl *et al*., 2008; Manawadu & Fernando, 2008; De Costa, 2010; Irangani & Shiratake, 2013). Photoperiod and temperature are two important environmental factors affecting rice flowering time and yield (Vergara & Chang, 1985; Luan, 2009). Extreme temperatures adversely affect vegetative development and growth duration (Lansigan *et al*., 2000; Craufurd & Wheeler, 2009; Wopereis *et al*., 2009; De Costa, 2010). Vegetative growth phase, reproductive phase and ripening phase are the three main phases of rice plant growth (Yoshida, 1981; Vergara & Chang, 1985; Wopereis *et al*., 2009). There are two sub-phases of vegetative growth phase: photoperiod insensitive basic vegetative phase (BVP), and photoperiod sensitive phase (PSP). The rice plant must attain a certain amount of growth in the BVP based on its response to photoperiod before it reaches the PSP (Vergara & Chang, 1985). Although there are several reports on estimates of the BVP and PSP, the transition from BVP to PSP is not well known (Chang *et al*., 1969; Vergara & Chang, 1985; Nishida *et al*., 2001).

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Temperature is an interrelated factor, which controls flowering time simultaneously with photoperiod (Vergara & Chang, 1985). The increase in ambient temperature advances the flowering time in crops (Jagadish *et al*., 2016). Three categories of *japonica* varieties of *Oryza sativa* were recognised based on their temperature and photoperiod sensitivity in different regions in Japan: photoperiod sensitive but temperature insensitive varieties from Hokkaido and Tohoku; photoperiod insensitive but temperature sensitive varieties from south-west Japan; and varieties distributed in all parts of Japan except in Hokkaido, which are sensitive to both photoperiod and temperature (Wada, 1942; Chandraratne, 1964).

Yoshida (1981) explained that the number of leaves is an indication of the physiological stage of rice plant. The vegetative phase of rice is also affected by the interactions of photoperiod and temperature (Summerfield *et al*., 1992; Lansigan *et al*., 2000; Wopereis *et al*., 2009). There are studies on responses of wheat cultivars to differences in photoperiod and temperature and their interactions at early vegetative stage (Major, 1980; Slafer & Rawson, 1994; Slafer & Rawson, 1996). Tollenaar and Hunter (1983) reported the effect of photoperiod and temperature on the number of maize leaves at different stages of vegetative growth. Determination of photoperiod sensitivity through leaf senescence and tiller removal was conducted by Best (1961).

Sri Lankan rice germplasm consists of a large diversity of early flowering and late flowering varieties, which are photoperiod-sensitive or insensitive (Chandraratna, 1953; 1954; Yoshida, 1983; Rathnathunga *et al*., 2016a; Pushpakumari *et al.*, 2017). Sri Lankan traditional rice *Oryza sativa indica* has been grown since ancient times, while Sri Lankan new improved rice has been bred through crosses between International Rice Research Institute (IRRI) accessions or crosses between Sri Lankan traditional rice. Wild rice species of *Oryza rufipogon* and *Oryza nivara* are the perennial and annual ancestors of *O. sativa* distributed in tropical and subtropical Asia (Khush, 1997; Shakiba & Eizenga, 2014). Seasonal sensitivity in some Sri Lankan traditional rice accessions (SLTRA) is a major drawback in farmer introductions and inclusion in breeding programmes. *Ma wee* (accessions 4561, 6699 and 3683) and *Maha ma wee* (8696) did not flower in the latter part of north eastern monsoon (*Maha*) in 2012/2013 during the experimental period of 200 days (towards more day-neutral days with approximately 12 hours of day-length) in Sri Lanka (Rathnathunga *et al*., 2016a). During late *Maha* (LM) in 2013/2014 of more day-neutral days and early *Maha* (EM) of more short days with less than 12 hours of day-length in 2014/2015, 43 *Ma wee* accessions (close to the number of total *Ma wee* collection at the Plant Genetic Resources Centre, Sri Lanka) were grown under natural field conditions to determine the flowering time variation among accessions. All accessions flowered during EM and only nine accessions flowered out of 43 accessions during the experimental period of ten months in LM (Pushpakumari *et al.*, 2017). There are no reports on the selection of rice accessions from Sri Lankan traditional rice germplasm for temperature sensitivity alone or for interaction of temperature and photoperiod for various agro-ecological systems as a remedy to future climatic fluctuations. Therefore, determination of varietal diversity in response to photoperiod and temperature at early vegetative growth could be useful in the selection of rice genotypes. In this study it was assumed that fifth leaf stage would be suitable to determine the vegetative growth responses as the first tiller emerges around the fifth leaf stage, usually making differences in the morphological structure of rice plant for flowering initiation (Yoshida, 1981; Moldenhauer & Slaton, 2001).

The objective of this experiment was to determine the varietal diversity of SLTRA in response to temperature and photoperiod at early vegetative growth. The information will be useful to reveal genetic factors for future breeding programmes on ecological adaptation to overcome adverse effects of climate change.

METHODOLOGY

Rice accessions

Thirty six SLTRA were selected for the experiment from the Sri Lankan traditional rice core collection based on morphological characterisation (Rathnathunga *et al*., 2016a): *Dahanala* (DN) 2049, *Duru wee* (DW) 4626, *Hondarawala* (HO) 3521, 3528, 4070 and 6428, *Kalu heenati* (KH) 4089 and 5485, *Kurulu wee* (KL) 3601, *Kiri murunga* (KM) 3828, 3865 and 4102, *Kaharamana* (KR) 4260, *Kalu wee* (KW) 5492, *Kottyaran* (KY) 5513, *Mada al* (MA) 3854, *Murungakayan* (MK) 3495 and 5610, *Mudukiriyal* (MU) 3970 and 4144, *Pachchaperumal* (PP) 5546 and 5550, *Sudu heenati* (SH) 3355, *Sulai* (SU) 3968, 4365, 6287 and 6346, *Sudu wee* (SW) 3462, 3858, 4195 and 4594, *Wanni heenati* (WA) 3401, *Ma wee* (MW) 4561, 6699 and 3683, and *Maha ma wee* (MM) 8696. Two randomly selected Sri Lankan improved rice varieties for low country of Sri Lanka (At 308 and Ld 368) and 2 Sri Lankan wild rice species (*O. nivara* and *O. rufipogon*) collected from the low country of Sri Lanka were also included for the experimental collection.

Greenhouse experiment and management practices

Rice accessions were grown under non-temperature controlled photoperiod chamber, with an average relative humidity of 80 % at the University of Ruhuna, Kamburupitiya, Sri Lanka in the, low country Wet Zone (WL2). The experiment was carried out under three photoperiod conditions in a completely randomised design (CRD) with 3 replicates: 8 h of light and 16 h of darkness (short day; SD), 12 h of light and 12 h of darkness (day neutral; DN) and 14 h of light and 10 h of darkness (long day; LD), during late July to mid-October, 2014 and late November, 2014 to mid-February, 2015. The light intensity was set at 1600 $\mu molm^{-2}s^{-1}$. Average monthly temperature was recorded during the two experimental periods. The seeds were sown in separate cups and the seedlings were transplanted on pots of 20 cm diameter after 21 ds. Fertiliser application was conducted according to the recommendation of the Department of Agriculture, Sri Lanka during 2014–2015: The basal dressing [of urea, triple superphosphate (TSP) and muriate of potash (MOP) as 50, 62.5 and 50 kg/ ha] and top dressings (of urea as 61.75, 123.5 and 123.5 kg/ ha) were applied as adjusted to pot size at 2 wks, 5 wks and 7 wks of planting, respectively. Manual weeding was done at regular intervals and the competition from weeds was kept minimal. The temperature was recorded daily and the monthly average temperature was calculated.

Measurements in fifth leaf stage of rice plant

Measurements were based on descriptors of rice (Rathnathunga *et al*., 2014). Three quantitative morphological characters were recorded as follows; days to fully expansion of fifth leaf (DFL), plant height (PH) and culm number at DFL (CN).

Statistical analysis

The average monthly temperature of trial 1 from July to October 2014 and trial 2 from November 2014 to February 2015 under greenhouse conditions were compared using t test. Boxplots and normal distribution curves were developed for DFL and PH for each treatment combination of SD, DN and LD at low temperature (LT) and high temperature (HT) regimes using Minitab software (version 14), USA. Univariate analyses of variance (ANOVA) was conducted using SAS (9.1 version) statistical software and significant differences (at $p < 0.05$) among treatments of photoperiod and temperature combinations were determined. Treatment means were separated using Duncan multiple range test (DMRT). Principal component analysis (PCA) and hierarchical cluster analysis by Ward's linkage (Onomo, *et al*., 2006; Giraldo, *et al*., 2010; Liu, *et al*., 2015) were performed using SPSS software (version 20), IBM, USA to determine the diversity among genotypes based on DFL and PH responses to treatment combinations of photoperiod and temperature.

RESULTS AND DISCUSSION

Temperature difference between trials in greenhouse

Average monthly temperatures of 36 ± 0.38 °C in July, 38 ± 0.45 °C in August, 37 ± 0.35 °C in September

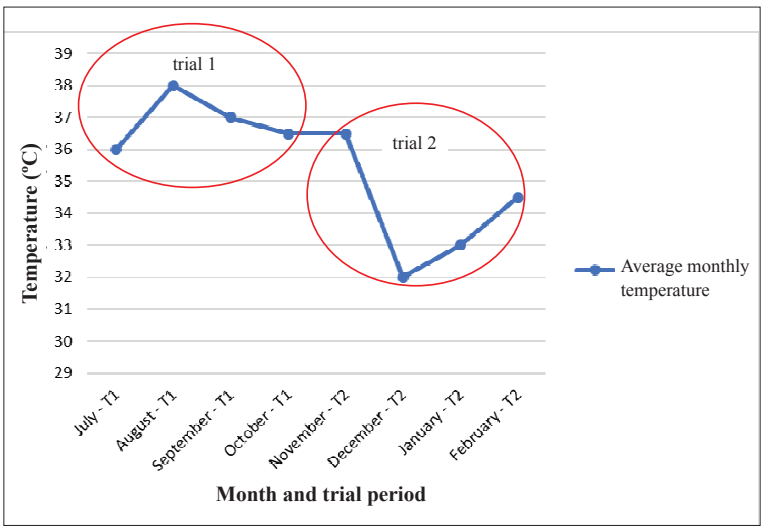


Figure 1: Natural temperature fluctuation during trial 1 (HT) and trial 2 (LT)

and 36.5 ± 0.54 °C in October, 2014 were recorded in trial 1 (Figure 1). The average monthly temperatures of trial 2 were 36.5 ± 0.56 °C in November, 32 ± 0.76°C in December, 2014, 33 ± 0.97 °C in January and 34.5 ± 0.67 °C in February, 2015.

The average monthly temperature (36. 9 ±0. 43 °C) of trial 1 (HT) from July to October 2014 was significantly higher than that of trial 2 (34.0 ± 0.98 °C) (LT) from November 2014 to February 2015 under greenhouse conditions ($p = 0.036$, $r^2 = 54.7$ % and coefficient of variance = 4.26 %). Except temperature, other conditions such as water content, wind velocity etc. were kept constant among the 3 photoperiods in the 2 trials.

Effect of photoperiod and trial temperature on DFL

A wide variation in DFL in response to photoperiod and temperature of the trials could be identified among the 36 SLTRA, 2 wild rice and 2 improved rice varieties. The frequency distribution of DFL for the treatments (of SD under HT and LT, DN under HT and LT and, LD under HT and LT) were normally distributed (Figures 2a and 3a). Irrespective of the photoperiod, average DFL under LT was significantly higher than that under HT. Average DFL at LT were 54 ± 1.10, 55 ± 1.19 and 62 ± 1.44 days under SD, DN and LD, respectively, where DFL under LD was significantly higher than those under SD and DN. DFL at HT were 42 ± 0.68, 44 ± 1.17 and

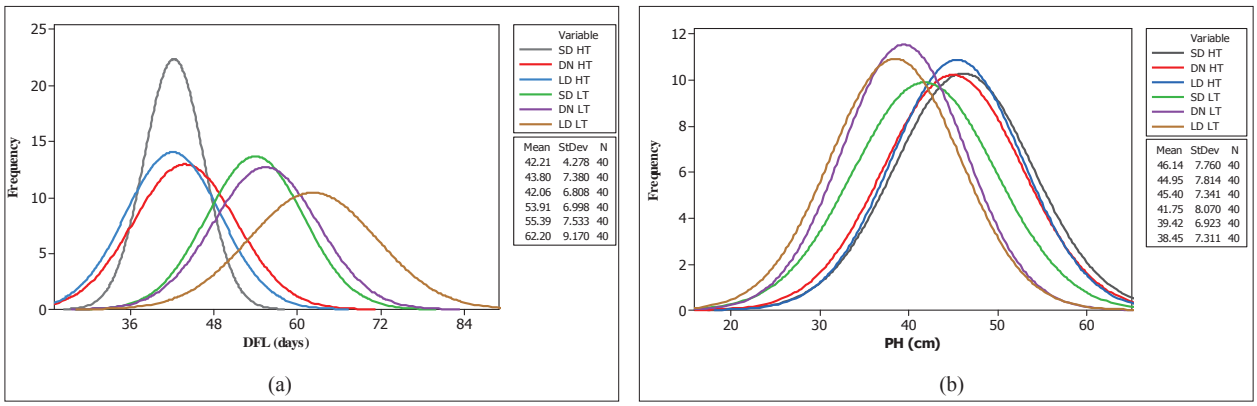


Figure 2: (a) Distribution of DFL of Sri Lankan traditional rice core collection under SD, DN and LD photoperiod conditions at LT and HT regimes; (b) distribution of PH of Sri Lankan traditional rice core collection under SD, DN and LD photoperiod conditions at LT and HT regimes.

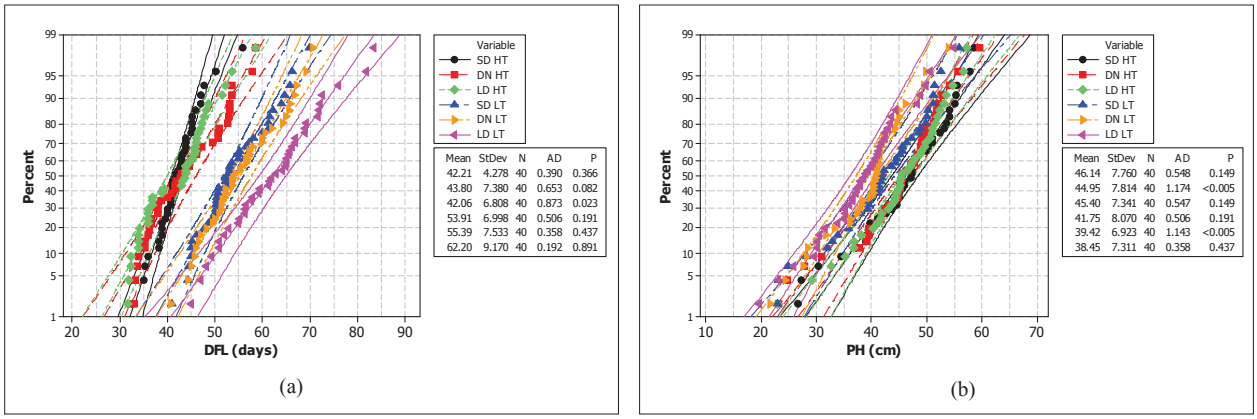
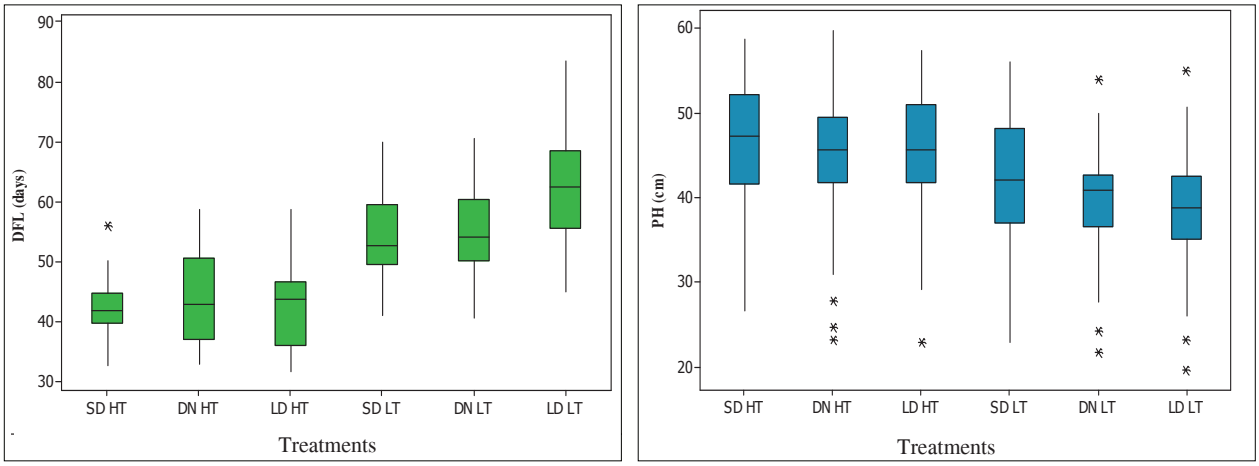
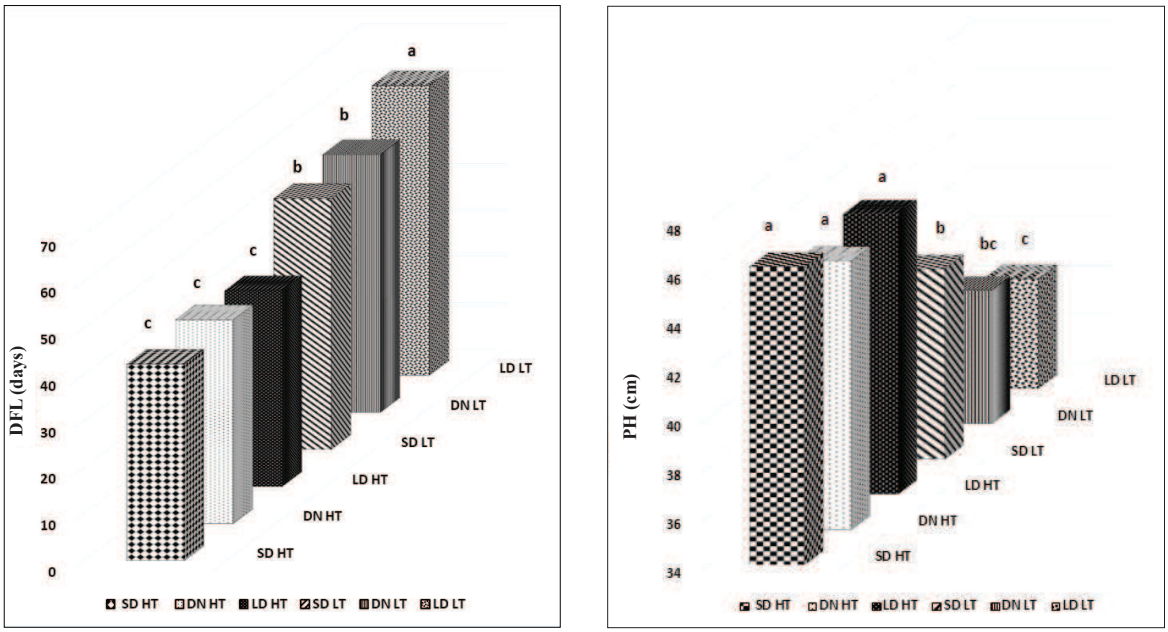


Figure 3: (a) Probability plot of DFL variation of Sri Lankan traditional rice core collection under SD, DN, LD photoperiod conditions at LT and HT regime; (b) probability plot of PH variation of Sri Lankan traditional rice core collection under SD, DN, LD photoperiod conditions at LT and HT regimes.



(a) (b)

Figure 4: (a) Effect of photoperiod and temperature on distribution of DFL in Sri Lankan traditional rice core collection in boxplots; (b) effect of photoperiod and temperature on distribution of PH in Sri Lankan traditional rice core collection in boxplots
Note: SDHT, DNHT and LDHT indicate SD, DN and LD photoperiods under HT, and SDLT, DNLT and LDLT indicate SD, DN and LD photoperiods under LT.



(a) (b)

Figure 5: (a) Effect of photoperiod and temperature on DFL in Sri Lankan traditional rice core collection; (b) effect of photoperiod and temperature on PH in Sri Lankan traditional rice core collection
Note: SDHT, DNHT and LDHT indicate SD, DN and LD photoperiods under HT, and SDLT, DNLT and LDLT indicate SD, DN and LD photoperiods under LT.

42 ± 1.08 days under SD, DN and LD, respectively (Figures 4a and 5a). High temperatures increase the growth rate of rice with vigorous tillering (Yoshida, 1973). Ambient growth temperature determines the rates of metabolic interactions and morphogenetic processes in the plant (Long *et al*., 1988). Several key phytohormones are affected by temperature leading to morphological responses (Bita & Gerats, 2013).

Table 1: Response of Sri Lankan traditional rice to photoperiod, trial temperature and their interactions on DFL

Traditional rice accession	R squared	CV value	P value	Photoperiod	Trial temperature	Photoperiod *trial temperature
Sulai 4365	61.60	12.63	0.0259*	0.011*	0.0637	0.4686
Hondarawala 4070	77.36	14.63	0.0014*	0.2146	0.0005*	0.0067*
Kiri murunga 3865	78.78	11.68	0.001*	0.0592	< 0.0001*	0.5061
Mada al 3854	72.57	15.82	0.0353*	0.5765	0.0026*	0.5364
Sulai 6287	86.80	10.12	< 0.0001*	0.4904	< 0.0001*	0.2618
Pachchaperumal 5546	91.59	7.18	0.0012*	0.3607	0.0002*	0.0057*
Hondarawala 6428	92.08	6.63	< 0.0001*	< 0.0001*	< 0.0001*	0.0558
Mudukiriyal 4144	93.83	7.16	< 0.0001*	< 0.0001*	< 0.0001*	0.412
Kalu wee 5492	70.74	14.94	0.006*	0.4171	0.0006*	0.1022
Kiri murunga 3828	60.59	12.57	0.0297*	0.3895	0.0018*	0.7676
Hondarawala 3521	58.88	13.12	0.037*	0.0574	0.029*	0.1984
Sudu wee 4594	84.04	8.38	0.0002*	0.0014*	0.5136	0.0002*
Wanni heenati 3401	89.10	6.14	< 0.0001*	0.0136*	< 0.0001*	0.0547
Dahanala 2049	52.81	18.31	0.0747	0.3699	0.0099*	0.4143
Murungakayan 3495	91.14	7.87	< 0.0001*	0.0183*	< 0.0001*	0.1694
Pachchaperumal 5550	80.06	12.87	0.0014*	0.1884	0.0006*	0.0047*
Duru wee 4626	62.09	14.92	0.0245*	0.176	0.008*	0.1044
Kalu heenati 5485	76.07	14.44	0.002*	0.3908	0.0003*	0.0241*
Sudu heenati 3355	48.84	21.39	0.1112	0.6024	0.008*	0.8518
Kalu heenati 4089	75.41	10.46	0.0134*	0.8494	0.0007*	0.5031
Sudu wee 3462	90.65	8.65	0.0001*	0.0491*	< 0.0001*	0.0006*
Kottyaran 5513	63.50	13.86	0.0198*	0.0471*	0.0078*	0.2901
Sulai 6346	87.50	15.14	0.0001*	0.113	< 0.0001*	0.0006*
Sulai 3968	84.25	17.10	0.0002*	0.0335*	< 0.0001*	0.0161*
Mudukiriyal 3970	89.25	10.71	< 0.0001*	0.3439	< 0.0001*	0.0877
Sudu wee 3858	49.11	11.05	0.1083	0.4078	0.0193*	0.3412
Kaharamana 4260	69.26	12.01	0.0078*	0.3088	0.0012*	0.0725
Sudu wee 4195	81.69	15.03	0.0004*	0.0224*	< 0.0001*	0.0373*
Murungakayan 5610	71.43	12.62	0.0052*	0.1032	0.0004*	0.6392
Kiri murunga 4102	69.29	13.61	0.0078*	0.2444	0.0008*	0.1577
Hondarawala 3528	67.90	13.58	0.0099*	0.0508	0.0016*	0.5397
Kurulu wee 3601	82.95	11.11	0.0003*	0.9898	< 0.0001*	0.9725
Ma wee 4561	73.50	11.73	0.0035*	0.0539	0.0005*	0.1862
Ma wee 6699	66.59	12.30	0.0193*	0.3124	0.0069*	0.0447*
Ma wee 3683	55.39	14.68	0.0563	0.1693	0.0118*	0.4013
Maha ma wee 8696	76.18	12.58	0.0065*	0.0672	0.001*	0.2132
At 308	72.99	12.38	0.0038*	0.0468*	0.0008*	0.1519
Ld 368	70.88	13.10	0.0058*	0.0866	0.0014*	0.0888
O. nivara	67.21	8.95	0.0111*	0.9473	0.0004*	0.6203
O. rufipogon	81.66	10.48	0.0009*	0.3748	< 0.0001*	0.028*

* $p < 0.05$ significant level

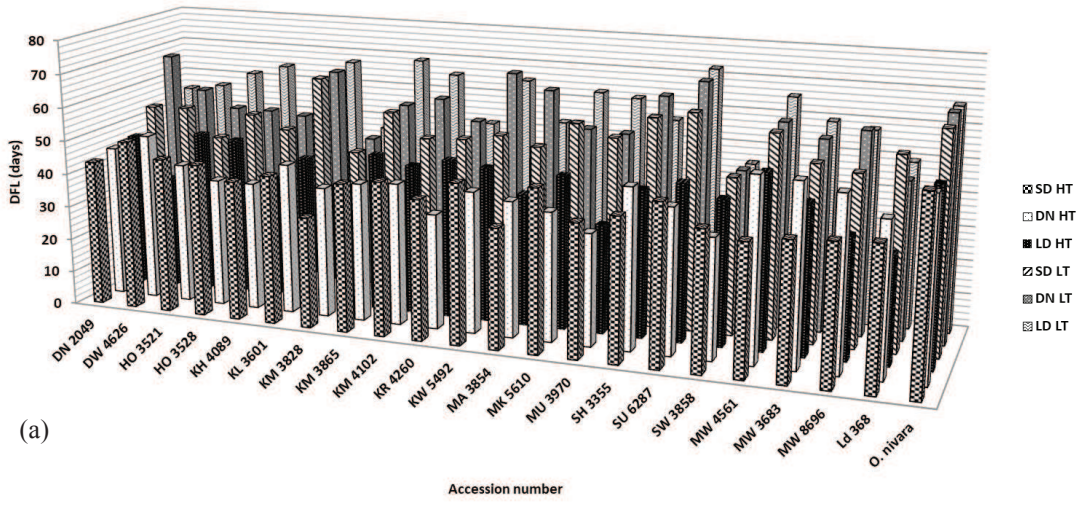
Increasing temperature advances flowering time in crops (Jagadish *et al*., 2016). However, according to the results, HT above optimum in trial 2 retards the growth rate during early vegetative stage with extended DFL. It will be of importance to determine if temperature differently affects early vegetative growth stages of rice as indicated here. Fei *et al*. (2017) reported that higher ambient temperature can promote auxin biosynthesis in *Arabidopsis* by enhancing ethylene signalling for root morphological responses. Unravelling the temperature signal transduction pathway in rice leading to vegetative growth rate control would be an important target for climate change breeding as flowering time is correlated with vegetative growth.

Effect of photoperiod, trial condition as temperature and their interaction on DFL was determined through ANOVA F test for each accession. Twenty two accessions (accessions 3865, 3828 and 4102 of *Kiri murunga*, 6287 of *Sulai,* 3854 of *Mada al*, 5492 of *Kalu wee*, 3521 and 3528 of *Hondarawala*, 4626 of *Duru wee*, 2049 of *Dahanala*, 3355 of *Sudu heenati,* 4089 of *Kalu heenati*, 3970 of *Mudukirial*, 3858 and 4195 of *Sudu wee*, 4260 of *Kaharamana*, 5610 of *Murungakayan*, 3601 of *Kurulu wee*, 4561, 6699 and 3683 of *Ma wee*, 8696 of *Maha ma wee,* Ld 368 and *Oryza nivara*) were affected by trial condition characterised by low temperature alone, which

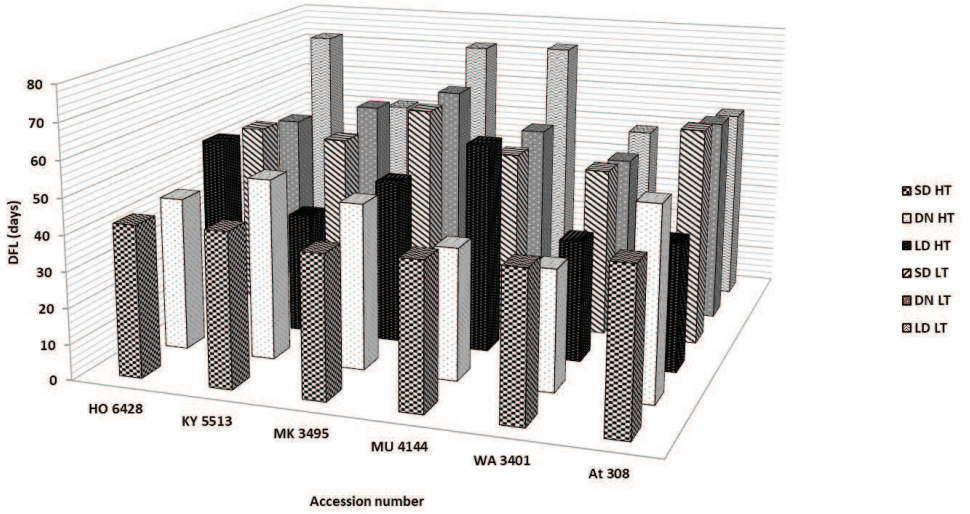
Table 2: Effect of photoperiod, temperature, photoperiod and temperature interactions within each variety on DFL

Accession and variety		High temperature regime in trial 1			Low temperature regime in trial 2		
		SD condition	DN condition	LD condition	SD condition	DN condition	LD condition
1	*Sulai* 4365	44 bc	36.3 c	48.3 ab	44.7 bc	44.3 bc	56.3 a
2	*Hondarawala* 4070	35 b	58.7 a	39 b	62.3 a	55.3 a	66 a
3	*Kiri murunga* 3865	43.7 c	41 c	47 bc	57.3 b	57.3 b	69 a
4	*Mada al* 3854	35.3 c	40 bc	39.3 bc	50.5 abc	65 a	53 ab
5	*Sulai* 6287	47 b	42.7 b	46.7 b	64 a	70.7 a	72.3 a
6	*Pachchaperumal* 5546	44 b	46.3 b	45.3 b	70 a	50 b	69 a
7	*Hondarawala* 6428	42.3 d	43 cd	53.7 b	52.3 b	49.5 bc	72 a
8	*Mudukiriyal* 4144	40.7 d	36.7 d	58.7 b	50.3 c	52 c	72.7 a
9	*Kalu wee* 5492	47 c	41.7 c	46 c	53 bc	69.3 a	65 ab
10	*Kiri murunga* 3828	32.7 b	38.7 ab	37 ab	44.3 a	46 a	47 a
11	*Hondarawala* 3521	46 b	41.7 b	48.7 b	45.3 b	52.3 ab	61.3 a
12	*Sudu wee* 4594	39 b	53.7 a	43.3 b	41 b	40.7 b	58 a
13	*Wanni heenati* 3401	41.3 b	33.7 c	34 c	47.7 a	45 ab	48.3 a
14	*Dahanala* 2049	43.3 b	45 b	46.3 b	53.3 ab	67.3 a	55 ab
15	*Murungakayan* 3495	39.7 c	46.3 c	46 c	61.3 b	62 b	71.7 a
16	*Pachchaperumal* 5550	40 bc	51 b	34.3 c	48.7 b	51.3 b	65.3 a
17	*Duru wee* 4626	50.3 a	49.7 a	34 b	53.7 a	57.3 a	56.7 a
18	*Kalu heenati* 5485	42.7 bc	44 bc	37 c	55 b	51 b	69.3 a
19	*Sudu heenati* 3355	42 b	47.3 ab	43.7 b	61.7 ab	65.7 a	56.3 ab
20	*Kalu heenati* 4089	41.3 bc	38 c	37 c	49.5 ab	51.5 a	52 a
21	*Sudu wee* 3462	43 b	35.3 c	31.7 c	50 b	47 b	61.7 a
22	*Kottyaran* 5513	43 ab	50.7 a	34 b	50.7 a	55.7 a	51 a
23	*Sulai* 6346	41.7 bc	36.7 c	32.3 c	45 bc	53.7 b	83.5 a
24	*Sulai* 3968	39 c	36 c	36 c	52.3 bc	56.7 b	82 a
25	*Mudukiriyal* 3970	39 b	33 b	32.3 b	55 a	53.7 a	62 a
26	*Sudu wee* 3858	40.7 ab	35.3 b	43 ab	46.3 a	45.7 a	45 a
27	*Kaharamana* 4260	41.3 bc	34 c	47.3 ab	51 ab	54 a	51 ab
28	*Sudu wee* 4195	36 bc	33.3 c	36 bc	45 bc	48.3 b	67 a
29	*Murungakayan* 5610	47.7 bcd	38 d	45.7 dc	58.3 ab	54.3 abc	63 a
30	*Kiri murunga* 4102	45.3 c	42 c	44.7 c	50.3 bc	60 ab	65.3 a
31	*Hondarawala* 3528	45.3 bc	38 c	47.7 bc	53.3 ab	52.3 ab	64.3 a
32	*Kurulu wee* 3601	44 b	44.7 b	44 b	66 a	66 a	67 a
33	*Ma wee* 4561	38.3 c	53.7 ab	51.7 b	60 ab	60.7 ab	65.7 a
34	*Ma wee* 6699	38.3 c	53.3 ab	44 bc	55.3 ab	51.7 ab	59.5 a
35	*Ma wee* 3683	40 c	53 abc	44 bc	52.3 abc	56.7 ab	59.3 a
36	*Maha ma wee* 8696	40.7 bc	50.7 ab	36 c	50.5 ab	60 a	57.7 a
37	At 308	45 bc	53.3 ab	36 c	61.3 a	58 a	55.3 ab
38	Ld 368	41.3 bc	44.7 b	32 c	56.7 a	46.7 ab	49.3 ab
39	*O. nivara*	56 bc	52.7 c	52.3 c	64.7 ab	66.7 a	66.3 a
40	*O. rufipogon*	45.3 c	58 b	46.3 c	66.3 ab	64.3 ab	76 a

Different letters indicate the different significant levels among photperiod treatments under each temperature trial in each accession



(a)



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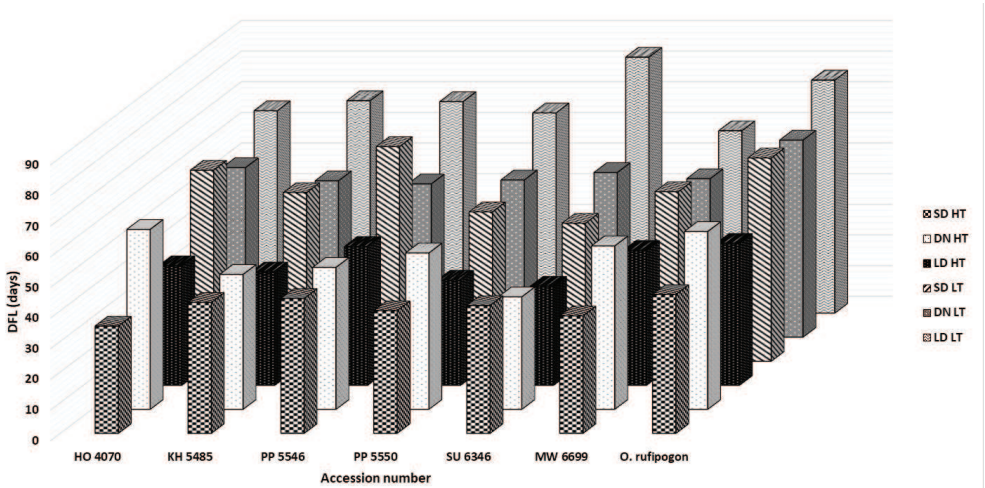

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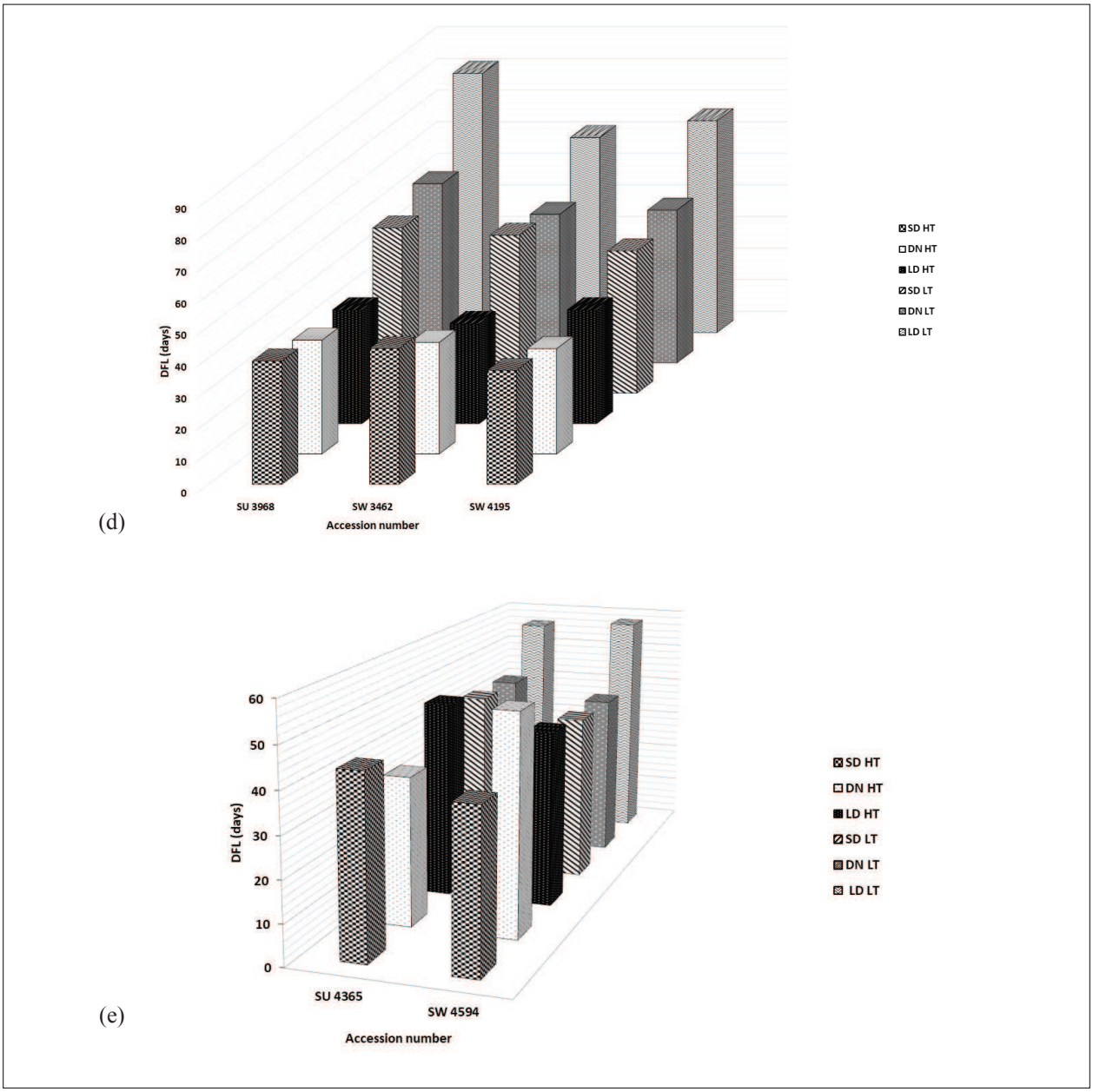
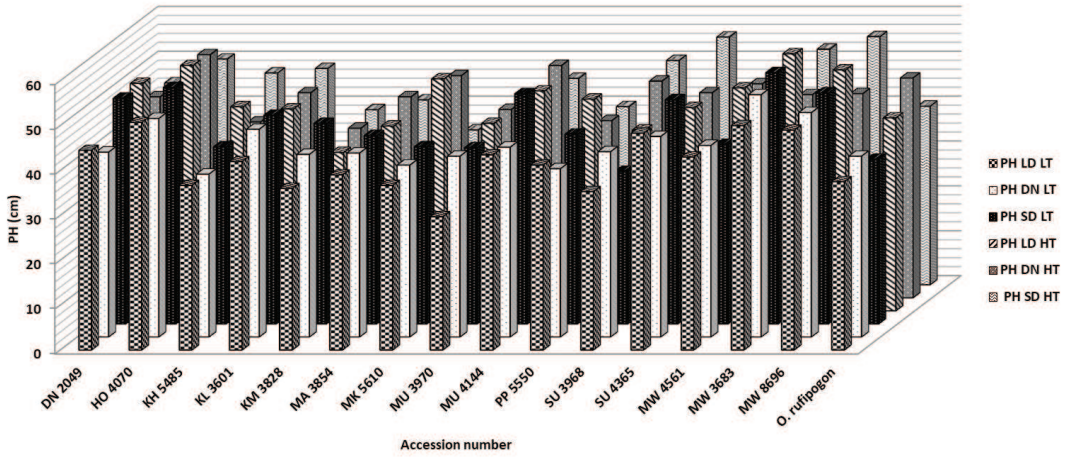
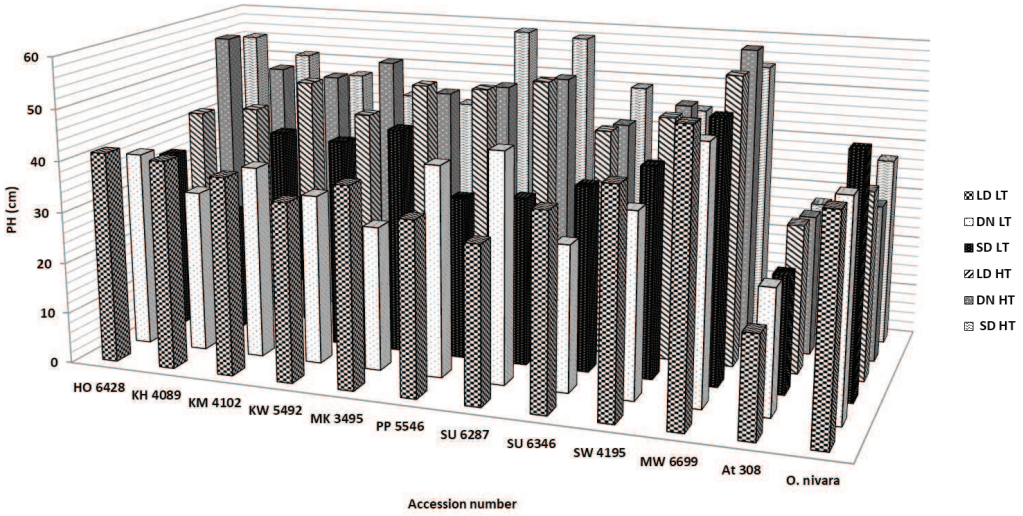


Figure 6: Effect of photoperiod and temperature on DFL of 40 Sri Lankan rice genotypes. Accessions affected by (a) temperature only; (b) photoperiod and temperature; (c) temperature and interaction between photoperiod and temperature; (d) photoperiod, temperature and interaction between photoperiod and temperature; (e) photoperiod only (*Sulai* 4365); photoperiod and interaction between photoperiod and temperature (*Sudu wee* 4594)

led to the extended DFL (Tables 1, 2 and Figure 6a). Photoperiod and trial temperature together affected accessions 6428 of *Hondarawala*, 4144 of *Mudukirial,* 3401 of *Wanni heenati,* 3495 of *Murungakayan,* 5513 of *Kottyaran* and At 308 (Figure 6b). Effect of temperature and interaction between photoperiod and temperature were identified in 7 accessions: 4070 of *Hondarawala*, 5546 and 5550 of *Pachchaperumal*, 5485 of *Kalu heenati,* 6346 of *Sulai*, 6699 of *Ma wee* and *O. rufipogon* (Figure 6c). Effect of photoperiod, trial temperature and their interaction were evident in accessions 3968 of variety *Sulai*, and 3462 and 4195 of variety *Sudu wee* (Figure 6d).



(a)



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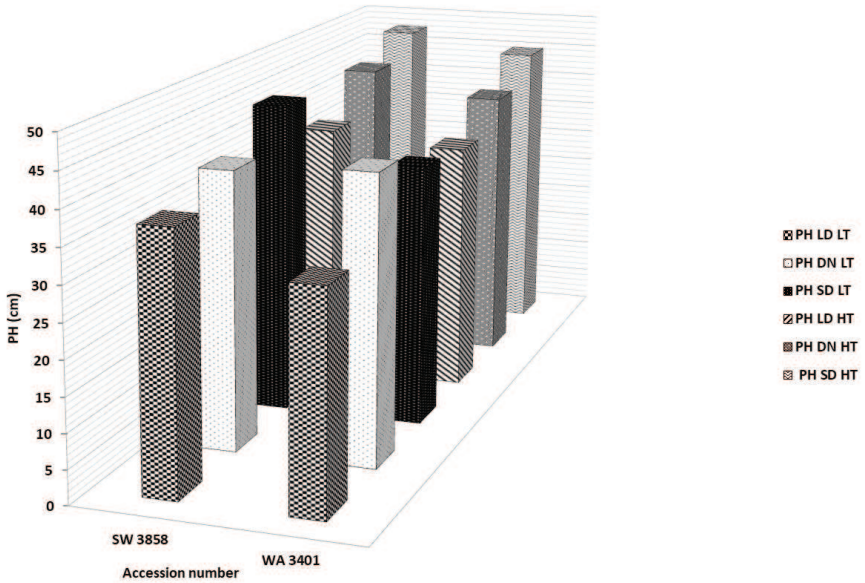

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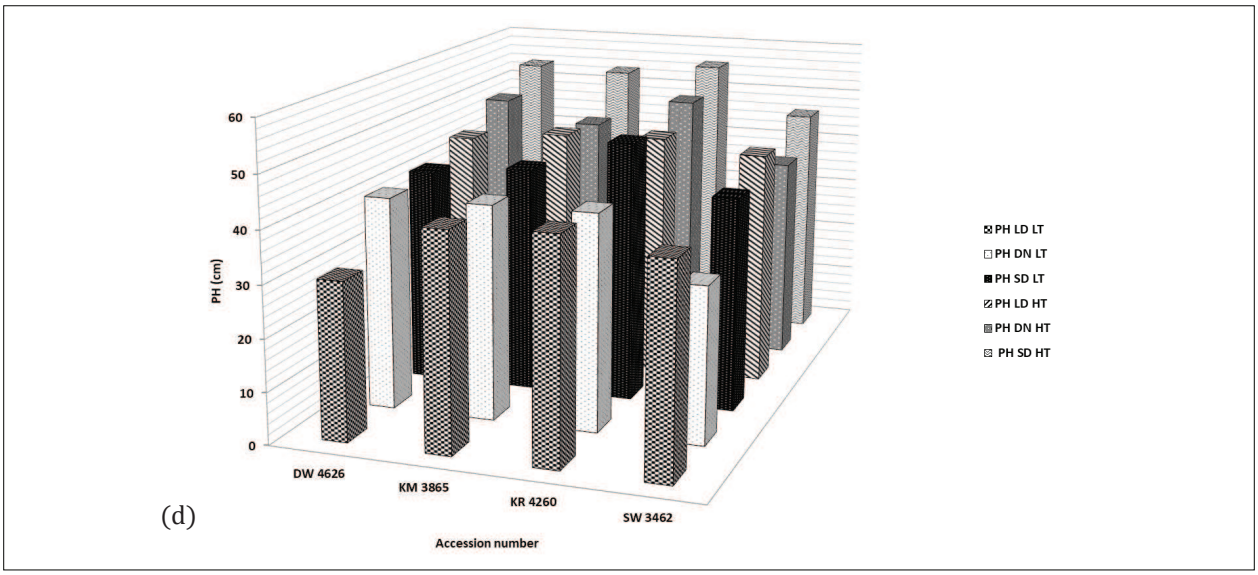

Figure 7: Effect of photoperiod and trial temperature on PH of 18 Sri Lankan traditional rice accessions from the collection. (a) Accessions did not respond to photoperiod, temperature or interaction; accessions responded to (b) temperature; (c) photoperiod; (d) photoperiod and temperature. p value = 0.001 (significant level at $p < 0.05$)

The photoperiod effect only on DFL was evident in one accession (4365 of *Sulai*) with increased DFL under LD (Figure 6e). The photoperiod and interaction between trial temperature and photoperiod were evident only in accession 4594 of *Sudu wee* (Figure 6e).

Under both HT regime in trial 1 and LT regime in trial 2, 6287 of *Sulai*, 3970 of *Mudukirial* and 3601 of *Kurulu wee* had similar DFL for all 3 photoperiods (Tables 1 and 2). Flowering times of the above accessions in a later stage were of variable pattern under a relatively low average monthly temperature to that of trial 1 in the above 3 photoperiods (*unpublished data*): in 6287 of *Sulai,* DFL was significantly early under SD and significantly delayed under LD conditions; in 3970 of *Mudukirial*, DFL was significantly delayed under SD and DN conditions and the accession 3970 did not flower during the experimental period of 350 days under LD; the accession 3601 of *Kurulu wee* did not flower under DN or LD conditions during the experimental period. The above results suggest further experiments on temperature and photoperiod effect on DFL of these accessions as the prominent photoperiod effect could be masked by high temperature.

Accessions 5546 of *Pachchaperumal*, 5492 of *Kalu wee*, 3521 of *Hondarawala*, 2049 of *Dahanala*, 3968 and 6287 of *Sulai* and 4102 of *Kiri murunga* had similar DFL under HT for all 3 photoperiods, while 4070 of *Hondarawala*, 3828 of *Kiri murunga*, 4626 of *Duru wee*, 5513 of *Kottyaran* and 3858 of *Sudu wee* had similar DFL under LT irrespective of photoperiod. The above results indicate the potential of early flowering in non-photoperiod responsive rice accessions during rising temperature in the environment. It is important to evaluate the reduction of yield in such accessions when affected by HT for short life span. Among different SLTRA, the reduction of yield has been previously observed with increasing DFL under field conditions (Rathnathunga *et al.*, 2016b, Rathnathunga & Geekiyanage, 2016). However, in photoperiod sensitive accessions of SLTR *Ma wee* under field condition during early SD season only, variation in DFL and yield were positively correlated revealing that vegetative growth, DFL and yield were affected by seasonal sensitivity (Pushpakumari *et al*., 2017). Vergara and Chang (1985) indicated that almost all *O. sativa indica* rice accessions mature in a shorter time under a SD photoperiod than under a LD photoperiod, where the degree of sensitivity varies greatly among accessions. According to Collinson *et al*. (1992), photoperiod sensitive inductive phase was increased under LD.

It will be important to determine the effect of temperature on vegetative growth amid photoperiod effect. Photoperiod and temperature are important

environmental factors affecting genetic factors of flowering time control in rice. The vegetative growth phase of rice comprises of photoperiod insensitive and photoperiod sensitive sub-phases, which are widely variable among accessions (Vergara & Chang, 1985; Collinson *et al*., 1992; Luan *et al*., 2009; Hatfield & Prueger, 2015). According to Rathnathunga *et al.* (2016a), DFL of *Sulai* accessions 3968, 4365, 6287 and 6346 during the latter part of SD season (late *Maha*) towards more DN days in 2013 at the Rice Research and Development Institute, Batalagoda were 61, 68, 57 and 133 days, respectively. During this experiment, DFL of

Table 3: Response of Sri Lankan traditional rice to photoperiod, trial temperature and their interactions on PH

Traditional rice accession	R squared	CV value	P value	Photoperiod	Trial temperature	Photoperiod * trial temperature
Sulai 4365	36.17	12.24	0.3057	0.1146	0.711	0.5074
Hondarawala 4070	20.73	9.94	0.6825	0.8965	0.3451	0.405
Kiri murunga 3865	68.81	7.31	0.0085*	0.0432*	0.0018*	0.3489
Mada al 3854	17.86	12.18	0.8701	0.5991	0.5903	0.8502
Sulai 6287	65.97	19.94	0.0136*	0.4972	0.0011*	0.202
Pachchaperumal 5546	78.20	12.56	0.0284*	0.3544	0.0037*	0.1806
Hondarawala 6428	63.22	16.89	0.0457*	0.37	0.0084*	0.1677
Mudukiriyal 4144	42.94	10.97	0.1891	0.7215	0.2126	0.0732
Kalu wee 5492	59.16	15.72	0.0357*	0.629	0.0057*	0.1186
Kiri murunga 3828	34.93	13.43	0.3311	0.1643	0.2385	0.7148
Hondarawala 3521	72.32	8.16	0.0044*	0.0089*	0.0206*	0.0273*
Sudu wee 4594	49.03	14.76	0.1092	0.1618	0.0688	0.2338
Wanni heenati 3401	52.89	12.68	0.074	0.0381*	0.1262	0.3822
Dahanala 2049	25.62	14.73	0.5541	0.4605	0.6849	0.3481
Murungakayan 3495	60.30	16.89	0.0308*	0.2064	0.0147*	0.0742
Pachchaperumal 5550	29.19	14.59	0.5106	0.3092	0.5608	0.4828
Duru wee 4626	88.12	7.56	< 0.0001*	0.0005*	< 0.0001*	0.2961
Kalu heenati 5485	34.99	17.07	0.3301	0.4034	0.0727	0.7362
Sudu heenati 3355	69.71	9.88	0.007*	0.5381	0.002*	0.0194*
Kalu heenati 4089	72.34	17.27	0.0217*	0.8831	0.0026*	0.0914
Sudu wee 3462	55.48	14.28	0.0557	0.0389*	0.034*	0.7394
Kottyaran 5513	48.81	18.44	0.1115	0.327	0.062	0.1354
Sulai 6346	47.33	21.81	0.1608	0.3916	0.0211 *	0.7404
Sulai 3968	38.22	22.41	0.2656	0.4485	0.0549	0.5676
Mudukiriyal 3970	63.96	9.96	0.0185*	0.0838	0.0249 *	0.0392*
Sudu wee 3858	48.70	11.37	0.1126	0.0255*	0.3351	0.8761
Kaharamana 4260	69.38	8.30	0.0077*	0.0109*	0.0042*	0.531
Sudu wee 4195	46.23	12.53	0.141	0.4744	0.0257*	0.3555
Murungakayan 5610	35.99	25.33	0.3093	0.4446	0.179	0.265
Kiri murunga 4102	54.87	12.26	0.0596	0.9183	0.0034*	0.5655
Hondarawala 3528	38.35	12.07	0.2631	0.9732	0.2515	0.089
Kurulu wee 3601	30.12	7.70	0.441	0.2006	0.4363	0.6676
Ma wee 4561	27.80	14.34	0.4985	0.6406	0.0805	0.9748
Ma wee 6699	43.84	8.91	0.2111	0.5534	0.0492*	0.3295
Ma wee 3683	33.18	13.20	0.3695	0.4816	0.6309	0.1676
Maha ma wee 8696	40.31	10.23	0.32	0.1864	0.5594	0.3418
AT308	69.29	10.51	0.0078*	0.5671	0.0006*	0.1474
LD368	61.73	10.06	0.0254*	0.0862	0.9002	0.0114*
O. nivara	42.06	18.89	0.1996	0.4341	0.0257*	0.804
O. rufipogon	37.37	16.08	0.3274	0.2829	0.1009	0.7762

* $p < 0.05$ significant level

Table 4: Effect of photoperiod, temperature, photoperiod and temperature interactions within each variety on PH

Accession and variety		High temperature regime in trial 1			Low temperature regime in trial 2		
		SD condition	DN condition	LD condition	SD condition	DN condition	LD condition
1	*Sulai* 4365	55.2 a	45.7 a	45.3 a	50 a	44.7 a	48.3 a
2	*Hondarawala* 4070	50.3 a	54.2 a	54.7 a	52.7 a	48.7 a	50.7 a
3	*Kiri murunga* 3865	53.2 a	45.3 b	46.7 b	43.7 b	41.3 b	41.5 b
4	*Mada al* 3854	41.2 a	44.8 a	41.2 a	42 a	41 a	39 a
5	*Sulai* 6287	58 a	51.7 a	53.3 a	33 b	45 ab	30.7 b
6	*Pachchaperumal* 5546	58.7 a	49.3 abc	51 ab	32 d	41.3 bcd	34 cd
7	*Hondarawala* 6428	54.3 ab	55.8 a	42 abc	35.8 c	38.5 bc	41.4 abc
8	*Mudukiriyal* 4144	46 a	51.8 a	49 a	51.3 a	42.3 a	43.5 a
9	*Kalu wee* 5492	43.7 ab	52.8 a	44.2 ab	41.2 ab	33.3 b	35 b
10	*Kiri murunga* 3828	39 a	37.8 a	35.3 a	44.7 a	40.7 a	36 a
11	*Hondarawala* 3521	51 a	41.7 bc	45.7 ab	45.3 ab	44.2 ab	35.3 c
12	*Sudu wee* 4594	30.5 a	24.7 ab	23 b	23.2 b	21.7 b	23.2 b
13	*Wanni heenati* 3401	45 a	41 a	36.8 ab	38 ab	41.8 a	31.5 b
14	*Dahanala* 2049	45 a	44.8 a	50.7 a	50.3 a	41.2 a	44.5 a
15	*Murungakayan* 3495	42.7 a	47.2 a	51 a	44.5 a	28.3 b	39.3 b
16	*Pachchaperumal* 5550	39.7 a	39.5 a	47.2 a	42.3 a	37.5 a	41.2 a
17	*Duru wee* 4626	53.7 a	49.2 ab	44.7 bc	41.7 c	41 c	30.3 d
18	*Kalu heenati* 5485	47.2 a	39.2 a	45.5 a	39.5 a	36.3 a	36.7 a
19	*Sudu heenati* 3355	47.3 ab	52.3 a	52.5 a	49 a	39.7 bc	38 c
20	*Kalu heenati* 4089	51 a	50 a	43.7 ab	25 c	31.8 bc	40.8 ab
21	*Sudu wee* 3462	46 a	39.5 ab	45.3 a	41.3 a	30 b	40 ab
22	*Kottyaran* 5513	47.3 a	42.5 ab	49.2 a	45.7 a	40.3 ab	30.2 b
23	*Sulai* 6346	48.5 a	43.3 ab	44.5 ab	36.5 ab	28.5 b	38 ab
24	*Sulai* 3968	50 a	48.3 a	40.3 a	34 a	41.3 a	35.3 a
25	*Mudukiriyal* 3970	39.5 a	42 a	41.8 a	39.3 a	40.3 a	29.7 a
26	*Sudu wee* 3858	47.7 a	44.3 ab	38.3 ab	45.7 ab	40.5 ab	37.3 b
27	*Kaharamana* 4260	55.5 a	51.2 ab	47.3 bc	50.2 ab	41.5 c	42.5 c
28	*Sudu wee* 4195	44.7 ab	48 a	48 a	41.3 ab	36 b	43.7 ab
29	*Murungakayan* 5610	34.5 a	49.5 a	51.7 a	39.5 a	38.3 a	36.7 a
30	*Kiri murunga* 4102	47.3 abc	49 ab	50 a	42 abc	37.8 c	38.7 bc
31	*Hondarawala* 3528	44.7 ab	46.7 ab	52 a	48.5 ab	45 ab	40.3 b
32	*Kurulu wee* 3601	48.2a	45.7 a	45 a	46.5 a	46.3 a	42 a
33	*Ma wee* 4561	45.7 a	47.7 a	49.7 a	40 a	42.7 a	43 a
34	*Ma wee* 6699	54.3 ab	59.7 a	56.8 ab	51.3 ab	49.5 b	55 ab
35	*Ma wee* 3683	52.5 a	45.3 a	57.3 a	56 a	54 a	50 a
36	*Maha ma wee* 8696	55.3 a	45.5 a	53.7 a	51.5 a	50 a	49 a
37	At 308	27.3 ab	27.8 ab	29.2 a	23 bc	24.3 abc	19.7 c
38	Ld 368	26.7 b	23.2 b	32.7 a	28.3 ab	27.7 ab	26 c
39	*O. nivara*	37.2 ab	31 b	36.8 ab	47.3 a	42 ab	42.5 ab
40	*O. rufipogon*	39.8 a	49 a	43 a	36.7 a	40.3 a	37.5 a

Different letters indicate the different significant levels of photoperiod treatments under each temperature trial in each accession

the above accessions under SD in trial 1 at HT were 39, 44, 47 and 41.7 days, while DFL under SD in trial 2 at LT were 52.3, 44.7, 64 and 45 days, respectively. The above results indicate the need for intensive studies on temperature and photoperiod interactions on vegetative growth and DFL of rice. Epistasis between flowering time genes *Se1* and *Ef1,* which coordinate changes of photoperiod sensitivity, basic vegetative phase and optimum photoperiod was studied by Nishida *et al*. (2001) and Uwatoko *et al*. (2008).

Effect of photoperiod and trial temperature on plant height at fifth leaf stage

The PH at DFL was considered as a vegetative growth parameter for biomass. A normal distribution in PH in response to photoperiod and temperature could be identified among 40 SLTRA, 2 wild and 2 improved rice varieties under SD, DN and LD, which varied from 32.7–56, 33–58 and 32–58.7 cm at HT and 41–70, 44.3–70.7 and 45–83.5 cm at LT, respectively (Figures 2b and 3b). The variation of PH was plotted as 6 curves representing the treatments (SD under HT and LT, DN under HT and LT and LD under HT and LT). The PH values under all treatments were normally distributed (Figures 2b and 3b). Irrespective of the photoperiod, average PH values under HT were significantly higher (46 ± 7.76, 45 ± 7.81 and 45 ± 7.31 cm under SD, DN and LD, respectively) than those under LT (42 ± 8.07, 39 ± 6.92 and 38 ± 7.31 cm under SD, DN and LD, respectively) (Figures 4b and 5b). The above results suggest that the effect of high temperature on harvest index could be adverse as vegetative growth is increased under HT.

However, 15 accessions: 4365 of *Sulai*, 4070 of *Hondarawala*, 3854 of *Mada al*, 4144 of *Mudukirial,* 3828 of *Kiri murunga*, 2049 of *Dahanala*, 5550 of *Pachchaperumal*, 5485 of *Kalu heenati,* 3968 of *Sulai*, 5610 of *Murungakayan*, 3601 of *Kurulu wee*, 4561 and 3683 of *Ma wee*, 8696 of *Maha ma wee* and *O. rufipogon* were not responsive to photoperiod or temperature in terms of PH (Tables 3 and 4; Figure 7a).

Temperature alone affected the PH of 12 accessions: 6287 of *Sulai*, 5546 of *Pachchaperumal*, 6428 of *Hondarawala*, 5492 of *Kalu wee*, 3495 of *Murungakayan*, 4089 of *Kalu heenati*, 6346 of *Sulai*, 4195 of *Sudu wee*, 4102 of *Kiri murunga*, 6699 of *Ma wee*, At 308 and *O. nivara.* Among those, only in *O. nivara,* the PH increased under LT (Figure 7b). Photoperiod effect was only detected in 3401 of *Wanni heenati* and 3858 of *Sudu wee* (Figure 7c). Temperature and the interaction between photoperiod and temperature were evident in 3355 of *Sudu heenati* and 3970 of *Mudukiriyal*. Photoperiod effect and trial temperature effect were evident in 3865 of *Kiri murunga*, 4626 of *Duru wee,* 3462 of *Sudu wee* and 4260 of *Kaharamana* (Figure 7d). All 3 effects of photoperiod, trial temperature and interaction between photoperiod and temperature were detected from 3521 of *Hondarawala* (Table 4).

Rathnathunga and Geekiyanage (2017) reported the differential response of *Ma wee* accessions 6702, 6699 and 3683 to photoperiod on PH at early vegetative phase. Pushpakumari *et al*. (2017) reported that the above 3 accessions were sensitive to late SD season remaining in vegetative phase without flowering. In a photoperiod experiment by Padukkage *et al*. (2017), PH was increased in LD only or/and DN photoperiod in 28 early flowering accessions of SLTR during flowering time irrespective of the flowering response in LD and DN. According to Endo-Higashi and Izawa (2011), ambient environmental conditions may partially control sink size through the action of the flowering time genes.

Regression analysis of days to fifth leaf and plant height

There is a significant relationship between plant height and flowering time (Lin *et al*., 2012). As DFL is affected by photoperiod and temperature, PH may be controlled by pleiotrophic effects of flowering time genes at flowering. Delayed flowering increases PH (Rathnathunga *et al*., 2016a). The negative regression relationship between PH and DFL (PH= 51.05-0.1675 DFL) (p value = 0.001) in this study suggests that during early vegetative phase, PH may be independent of flowering time gene effect (Figure 8).

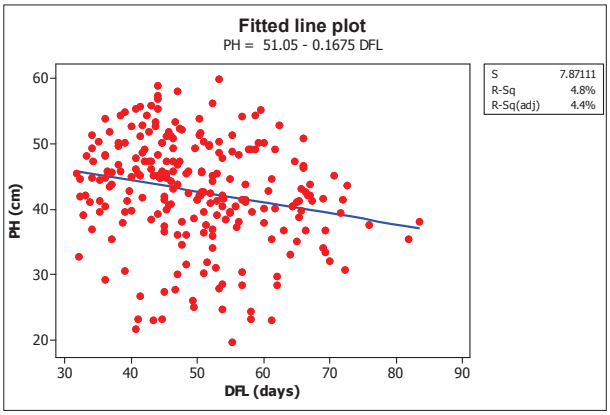

Figure 8: Regression analysis for relationship of DFL and PH of 40 Sri Lankan traditional rice accessions irrespective of temperature or photoperiod effect.
p value = 0.001 (significant level at $p < 0.05$)

Effect of photoperiod and trial temperature on culm number at fifth leaf stage

The CN of the rice collection was neither affected by photoperiod nor temperature at fifth leaf stage. Padukkage *et al*. (2017) have previously reported that CN of very early flowering SLTRA was also not affected by the same photoperiod conditions. The effect of environmental factors on CN may vary on the environment, genotype

and growth stage of rice. Pushpakumari *et al*. (2017) reported that the total CN of photoperiod sensitive *Ma wee* accessions at flowering was dependent on genotype and interaction between genotype and photoperiodic season under field conditions. Production of extremely high CN in SLTR variety *Dewaraddili* under LD condition was reported by Geekiyanage *et al*. (2012) under greenhouse condition.

Table 5: The major principal components through PCA of Sri Lankan rice collection based on response to photoperiod and temperature

PC	PC 1	PC 2	PC 3
Contribution to variation	39.5 %	20.0 %	15.5 %
Composition of characters	PH at HT under SD (0.758)	DFL at HT under DN (0.635)	DFL at HT under DN (0.531)
	PH at HT under DN (0.818)	DFL at LT under SD (0.837)	DFL at LT under LD (- 0.656)
	PH at HT under LD (0.897)	DFL at LT under DN (0.694)	
	PH at LT under SD (0.757)		
	PH at LT at DN (0.858)		
	PH at LT under LD (0.812)		

Varietal diversity in response to photoperiod and trial temperature

Varietal diversity on differential response to photoperiod and temperature for vegetative growth though DFL and PH among tested SLTRA varieties could be detected. A principal component analysis (PCA) was performed for DFL, PH and CN of accessions under 3 photoperiods in each trial temperature. Seventy five percent of the total observed variation was explained by three principal components (PC), where PH under all treatments was included in PC1 (Table 5).

There were 2 main clusters at rescaled distance of 25 in the dendogram (Figure 9). Wild rice and all SLTRA excluding accession 4594 of *Sudu wee* were in the first cluster. Improved varieties (Ld 368 and At 308) and *Sudu wee* 4594 were included in the second cluster. In the first cluster, *Sudu wee* 3462 and 4195, *Hondarawala* 3521 and 3528, *Kiri murunga* 3865 and 4102, *Sulai* 6346 and 3968 *Ma wee* 3683 and 6699 and, *O. nivara* and *O. rufipogan* were grouped as pairs into sub-clusters at a rescaled distance less than 5. Accessions 3683, 6699 and 4561 of *Ma wee*, 4070 of *Hondarawala*, 2049 of *Dahanala*, 3601 of *Kurulu wee* and 8696 of *Maha ma wee* that did not flower or flowered very late during core collection development (Rathnathunga *et al*, 2016a) were included in one sub-cluster of the first cluster at a rescaled distance close to 10.

The second major cluster comprised of the 2 improved varieties (Ld 368 and At 308) and *Sudu wee* 4594, which was morphologically close to improved rice in terms of plant architecture, yield components and DFL in all 3 photoperiods (Rathnathunga *et al*., 2016).

Identification of genetic factors associated with the diversity in temperature and photoperiod responses at early vegetative phase in terms of DFL and PH in the SLTRA would provide breeding materials for future work.

CONCLUSION

Naturally fluctuating LT (34.0 ± 0.43 ^{0}C) extended the average DFL of 40 Sri Lankan rice genotypes significantly over that under HT (36. 9 ± 0.98 ˚C) irrespective of photoperiods. Among SLTRA the effect of temperature on DFL was more common (on 22 accessions out of 40) over that of photoperiod on DFL (one accession out of 40).

HT extended the average PH significantly in contrast to LT in the collection of 40 Sri Lankan rice genotypes. Fifteen accessions were not responsive to photoperiod or temperature on PH at DFL stage. Temperature alone affected 12 accessions and photoperiod alone affected 2 accessions. Increased DFL reduced the PH as indicated by regression relationship of PH = 51.05–0.1675 DFL, suggesting the common phenomenon that extended vegetative period due to late flowering increases PH, is not valid during early vegetative phase.

In hierarchical cluster analysis after PCA based on DFL and PH variation in response to temperature and photoperiod, SLTRA and wild rice were included into one cluster except for *Sudu wee* 4594 at rescale distance of 25, which was close to improved rice in morphology, and was included into the second cluster with improved rice.

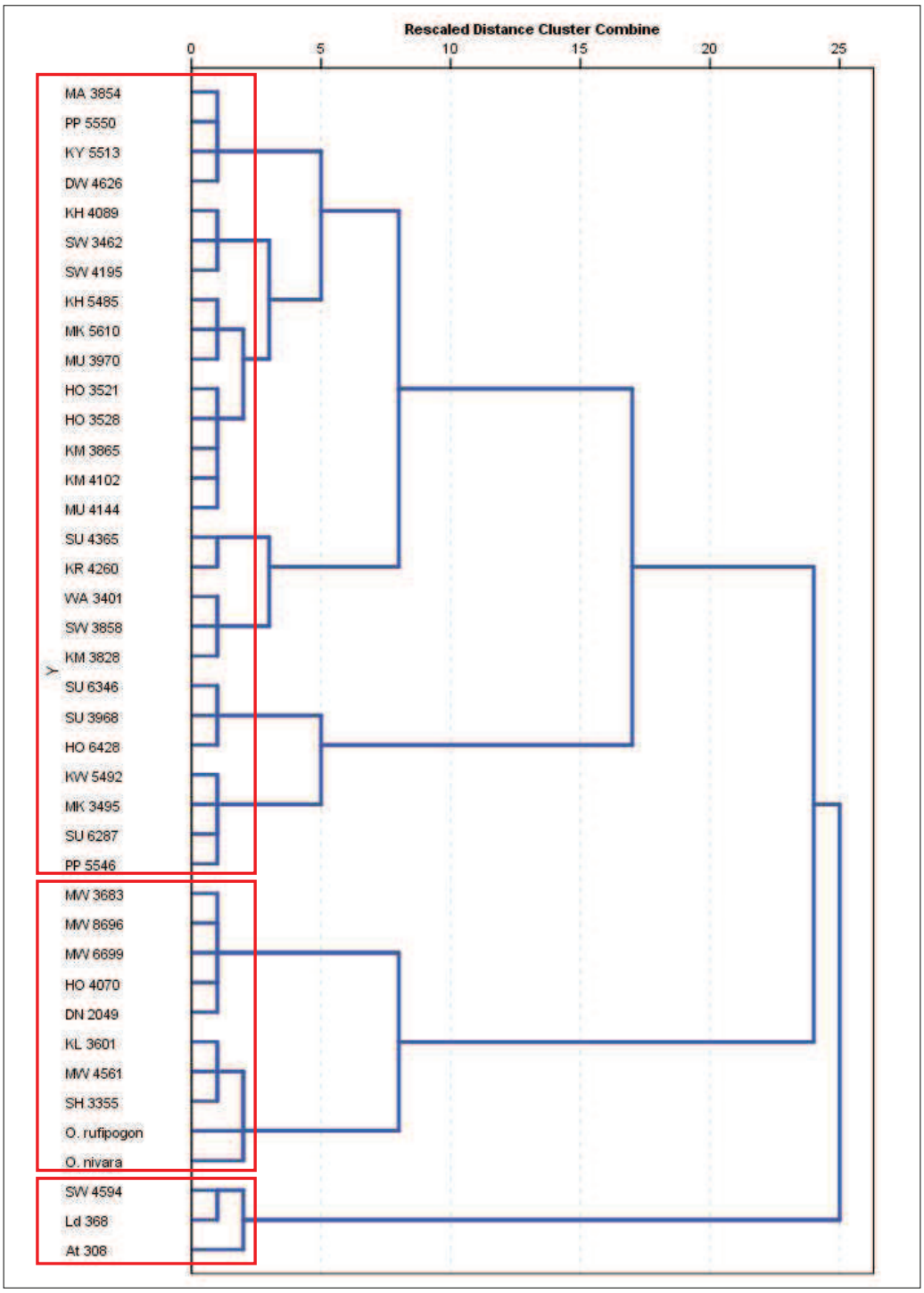

Figure 9: Diversity of experimental collection of 36 SLTRA, 2 improved rice and 2 wild rice on response to photoperiod and temperature based on the dendogram derived through cluster analysis

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