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ARTICLE

Diversity of Flower Opening Time and Duration in Rice (*Oryza sativa* ssp. *indica*) Landraces of South and Southeast Asia in Different Cultivation Seasons

***Debal Deb*[1*], *Niranjan V Joshi*[1,2], *Debdulal Bhattacharya*[1], *Mahendra Nauri*[1], *Rakesh Ganguly*[1]**

[1] *Basudha, Centre for Interdisciplinary Studies, Kolkata, 700068, India*

[2] *Energy and Wetlands Research Group, CES TE 15, Indian Institute of Science, Bangalore, 560012, India*

ABSTRACT

Different cultivars of rice (*Oryza sativa*) open at different times of the day, and the overlap of anthesis time in rice between the neighbouring cultivars is of crucial importance to the degree of cross pollination in rice. Nevertheless, none of the past experiments with cross pollination between different rice cultivars ever reported the respective flower opening time (FOT) and flower exposure duration (FED) of the parent cultivars, until recently. The authors present here the first record of FOT and FED of 1114 *indica* rice landraces of South and Southeast Asia, growing during summer and winter seasons in three consecutive years. The authors also present an analysis of the influences of the growing season on the anthesis behaviour, and present the first records of the FOT and FED variability on sunny and cloudy days of a large number of landraces. The data show that rice florets tend to open earlier in the morning (that is, take a shorter time to anthesis after sunrise) on sunny days than on cloudy days, and also significantly later during long day seasons (spring and summer) than during short day season (winter); and that FED is inversely related to both FOT and the length of duration from sunrise to first flower opening. The wide ranges of FOT (8:50 a.m. to 12:40 p.m.) and FED (15 to 194 minutes) also suggest the ample time window for receiving pollen from neighbouring cultivars with different FOT, enhancing the chances of cross pollination between hundreds of rice landraces with FOT and FED overlaps.

Keywords*:* Anthesis; Flower opening time; *Indica* landraces; Pollination; Rice; Season

*CORRESPONDING AUTHOR:
Debal Deb, Basudha, Centre for Interdisciplinary Studies, Kolkata, 700068, India; Email: debdebal@gmail.com

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1. Introduction

The flower opening time (FOT) and the duration of the flowers remaining open (= flower exposure duration, FED) are crucially important for the success of pollination and fertilization in rice (*Oryza sativa* L.) plants. Although rice is widely known to be predominantly self-pollinating, our recent study [1] showed that cross-pollination can occur at a high frequency between cultivars with a large temporal overlap of FED. In cross pollination experiments, published since the early last century, the FOT and FED of the cultivars were never recorded. It seems likely that the FED of the pairs of cultivars chosen in those experiments were non-overlapping, resulting in their reporting of extremely low (0 to 2%) frequency of cross-pollination between different rice cultivars [1]. The knowledge of FOT and FED is of crucial importance, both for the purpose of preventing cross-pollination between neighbouring cultivars, and to ensure cross-pollination success in hybridization experiments. Indeed, if the florets of the ovary parent (OP) close even a second before the FOT of the pollen parent (PP), the FED overlap between the two parents is zero, and consequently, there would be no cross pollination. In spite of the crucial importance of FOT and FED overlap between the OP and the PP, none of the reports of cross pollination experiments, published since Beachell et al. [2] till Somaratne et al. [3], surprisingly mention any of these three important parameters: FOT, flower closing time (FCT), and FED of the cultivar pairs selected in the respective experiments.

The earliest record of FOT in cultivated rice was made by Stok [4], informing that in Java, flowers of many rice cultivars opened between 0900 h and 1000 h, while some opened between 1200 h to 1300 h. Pope [5] reported that in the US, rice florets fully opened at 1014 h, and closed at 1300 h. A more recent study [6] reports that the beginning of the FOT of Nanjing 11 in temperate Japan was at ca. 0900, and the FOT of IR64 in the Philippine tropics began at ca. 1100.

There is a paucity of FOT and FED data for *O. sativa* ssp. *indica* landraces, of which the first record of FOT is found in Sharngapani [7], who noted that *aus* rice varieties (flowering in April-May) open at ca. 0700 h, while the winter rice cultivars, flowering in September-October, opened at ca. 0900 h. A large number (n = 289) of Asian cultivars, including some landraces from South and Southeast Asia, are reported to open their florets between 2.35 h and 5.08 h after sunrise during the dry hot season, compared to 3.05 h and 5.50 h after sunrise during the wet colder season in southern India [8]. However, the exact time of FOT is not available from their data. A later examination [9] of FOT and FCT of both *indica* and *japonica* cultivars, totalling 93, including 17 South Asian cultivars (12 from India, 2 from Nepal and 1 each from Bangladesh, Bhutan and Sri Lanka) revealed that the FOT of the *indica* cultivars, all grown in Japan, ranges between 0953 h and 1116 h.

A brief range of FOT data, gathered from published literature (summarised in **Table 1**) indicates that flowers of *indica* varieties tend to open earlier than *Japonica* varieties in similar latitudes. However, The FOT of a cultivar native to lower latitudes (e.g. southern India) is apt to be delayed in northern latitudes (e.g. in the US and Japan), due to lower temperatures and shorter day length. Anthesis of winter rice cultivars of South Asia would begin too late at the cold northern latitudes, "because frost will set in before harvest" [10]. This corroborates an earlier report [11] that a majority of flowers of 12 rice cultivars of Asian origin opened between 1200 h and 1400 h in California, while only 0.53% of the florets of these cultivars opened between 1600 h and 1700 h. While these reports indicate a wide diversity of FOT in rice cultivars in different geographical locations, the corresponding data of flower closing time (FCT) and the duration of the rice florets remaining open (FED) are not available. Here we contribute to expanding the database of FOT, FCT and FED of landraces, and constitute the first comprehensive report of FOT and FED of 1114 *indica* landraces cultivated in South and Southeast Asia.

Table 1. Published records of the earliest and last FOT (local time) for rice cultivars from different countries.

Country of origin	*Indica*		*Japonica*		Reference
	Earliest FOT	Last FOT	Earliest FOT	Last FOT	
China	09:01	10:47	11:44	12:02	[9]
Bangladesh	10:47	-			[9]
Japan			08:00 to 09:00	16:00 to 17:00	[11]
	10:08	11:42	10:19	12:35	[9]
India	07:00	12:00			[7]
	09:53	11:16			[9]
Indonesia	09:00	13:00			[4]
	10:44	12:00	11:01	-	[9]
Myanmar	07:00	09:00			[12]
	10:38	11:31			[9]
Nepal	10:51	11:30			[9]
Philippines			09:00	11:30	[13]
	09:55	11:15			[9]
USA			10:00 to 12:00	14:00 to 16:00	[11]
			10:10	11:42	[9]

2. Materials and methods

2.1 Study site and materials

A total of 1140 landraces were grown for this study on the Basudha conservation farm (http://cintdis.org/basudha), located in Bissam Cuttack block, Rayagada district of southern Odisha (19°42’32.0” N, 83°28’8.4” E). However, owing to the lack of adequate resources and field hands, we were able to document the complete flowering data of 1114 landraces, which comprise the materials for this study. All these landraces, originally collected from different districts of Bangladesh, India, Myanmar, Nepal, Pakistan and Sri Lanka, in addition to 18 landraces from Southeast Asia and 2 from East Asia (**Table 2**), were subjected to phenol reaction test and endosperm translucence examination for amylose [14,15], based on which we detected the presence of only five *Japonica*-type landraces (0.45%) in our sample, amongst whom one was accessed from Italy, 1 from South Korea, 1 from Myanmar and 2 from India. We added the Korean and Italian cultivars as references for characters of the South Asian *japonica* landraces.

2.2 Study period and seasons of cultivation

All landraces were sown during the *aman* season (sown in June, harvested from September to February of 2020 with 969 landraces, followed by 31 landraces during *boro* (sown in January, harvested during mid-summer during May-June) of 2021, 117 landraces during *aman* of 2021, 49 landraces during boro of 2022, and 5 landraces during *aus* season (sown in March, harvested in late summer to Autumn in June-July) of 2022, and 389 landraces during *aman* of 2022 (See **Table 3** and **Table 4**). During each growing season, all the rice seeds were sown within 6 days in nursery beds for germination. After germination, 14 to 16-day-old seedlings of each landrace were transplanted in an 8 × 8 matrix, at $16/m^2$ density, in a 4 m^2 farm plot, where the soil had been prepared following standard organic method, with no synthetic agrochemical inputs. We followed the steps described below, to record the flower opening time (FOT) and closing time (FCT) in each discrete varietal plot:

Among the *aman* 2020 landraces (harvested in winter 2020), 29 were sown successively during *boro* 2021, and 22 *aman* 2021 landraces were sown in succeeding *boro* 2022. Further, 8 landraces were repeated between *boro* and *aman* of 2021, and 73 landraces between *boro* and *aman* of 2022. **Table 4** summarises the sowing schedules. A total of 58 landraces were harvested in summer (*boro* and *aus*) seasons of 2021 to 2022, whereas a total of 1111 *aman* varieties were harvested in winter from 2020 to 2022.

Table 2. Countries of origin of the 1114 landraces cultivated in different seasons.

Country	No. of landraces		
	Aman (winter harvest)	*Boro* and *aus* (summer harvest)	All seasons
Bangladesh	39	1	39
India	1017	54	1020
Myanmar	3	0	3
Nepal	2	0	2
Pakistan	1	1	1
Sri Lanka	30	1	30
Philippines	15	0	15
Thailand	2	0	2
South Korea	1	0	1
Italy	1	1	1
Total	**1111**	**58**	**1114**

Table 3. Life history stages of the *aman*, *boro* and *aus* landraces.

Season	No. of landraces examined	Sowing dates	Transplanting dates	Flowering dates	Harvesting dates
Aman 2020	969	15 Jun-30 Jun	6 Jul-16 Jul	8 Aug-22 Jan	2 Sep-5 Feb
Boro 2021	31	20 Jan-23 Jan	5 Feb-12 Feb	2 Apr-5 May	30 May-3 Jun
Aman 2021	117	28 Jun-4 Jul	15 Jul-19 Jul	1 Sep-22 Oct	17 Sep-2 Jan
Boro 2022	47	20 Jan-23 Jan	6 Feb-11 Feb	4 Apr-6 May	2 Jun-8 Jun
Aus 2022	5	3 Mar	3 Apr	27 May-21 Jun	25 Jun-9 Jul
Aman 2022	391	21 Jun-31 Jun	10 Jul-18 Jul	31 Aug-27 Nov	13 Sep-8 Jan

Table 4. Schedule of sowing of 1114 landraces from winter 2020 to winter 2022. Numbers above the diagonal are the number of varieties repeat-sown in different cultivation seasons.

Cultivation season	***Aman* 2020**	***Boro* 2021**	***Aman* 2021**	***Boro* & *Aus* 2022**	***Aman* 2022**
Aman 2020	**969**	30	108	48	258
Boro 2021		**31**	8	23	18
Aman 2021			**117**	22	5
Boro & *Aus* 2022				**50**	22
Aman 2022					**390**

2.3 Procedure of data recording

A total of 1114 landraces were sown, among which 717 landraces were cultivated only once over the entire study period of 3 years (2020 to 2022). To record the variations of flower opening time and duration in different seasons and in different light conditions, 397 landraces were repeatedly cultivated in different seasons. Some of the landraces, which were attacked by pests in the nursery were also grown in replicated plots during the same season and in the same year. The procedure of recording the time and duration of anthesis of each landrace is as follows:

a) As flowering typically begins one day after heading [16,17], we prepared for recording the time of anthesis soon after recording the heading date and time. We recorded the time of opening of the first (apical) floret in the first emerged panicle in each landrace population (consisting of 64 plants), and recorded the time of each event, before moving on to another plot that was also expected to open on the same date.

b) We often missed the FOT of several cultivars that simultaneously flowered on the same day at the same time. Over three years (2020-2022) of the study, we were able to record the FOT and FCT of a total of 1114 rice landraces.

c) After recording the FOT of each varietal population, we re-visited the same plot regularly to record the FOT and FCT of the last florets of the same panicle. The length of time between the FOT of the first floret and the FCT of the last florets in a panicle indicates the exposure duration (FED) of a variety's florets.

d) If the florets of the first emerged panicle opened and/or closed on a cloudy day, we also recorded both the FOT and FCT of other florets on another panicle of the same cultivar on a subsequent sunny day. This was not possible for every cultivar, so the number of observations of FOT and FCT on sunny and cloudy days was not equal.

e) The length of sunrise-to-anthesis duration (SAD) was estimated from the local sunrise time on each day of anthesis. The exact sunrise time at Bissamcuttack Block was obtained from https://www.timeanddate.com/sun/@10775335 and https://isubqo.com/prayer-time/india/odisha/bishama-katek.

The FOT and FED of all the cultivars were recorded, generating a total of 1660 data points (including data on flowering on sunny and cloudy days of the cropping seasons of 2020, 2021, and 2022). All these data are available on Harvard Dataverse [18], which is the first comprehensive database of the range of FOT, FED, and the length of time after sunrise until the anthesis of 1114 *indica* rice landraces.

2.4 Statistical analyses

All analyses were made on a desktop using Open Office Calc program on Linux-Max. The distribution of data was examined using Shapiro-Francia *W'* and Anderson-Darling *W* tests, which are more sensitive and powerful than other tests of normality [19,20]. When the normality assumption was not supported, we employed the Mann-Whitney *U* test to test the significance of the difference between means. We chose $p < 0.01$ for the level of significance as well as confidence intervals for all $df > 50$.

3. Results and discussion

We present here the first description of the range of FOT of 1114 *indica* rice landraces and the variability of flower opening behaviour of a portion of these landraces on both sunny and cloudy days from September 2020 to February 2022. For the convenience of usage, we shall henceforth describe the colder long day seasons of flowering as "winter" and hotter long day seasons as "summer", although some calendar months may not strictly correspond to these shorthand terms.

3.1 Frequency distribution of FOT during summer and winter

The *aman* type landraces are characterized by their flowering during the progressively shortening day length in colder months (September to January). In all three years (2020, 2021 and 2022), the peak of anthesis of these landraces occurred in early October.

The flowering of a majority of *boro* and *aus* landraces peaked in the middle of April (**Figure 1**). As the sunrise hour changes with the season, the length of time from a sunrise hour to FOT varies with the cultivation seasons. The sunrise to anthesis duration (SAD) for *aman* rices (of 2020, 2021 and 2022 combined) flowering in winter and that of the *boro* and *aus* landraces flowering in summer (of 2021 and 2022 combined) are shown in **Figure 2**. During summer, anthesis frequency reaches a peak between 290 min and 300 min after sunrise, whereas during winter months, the frequency is the highest between 260 min and 270 min after sunrise. Thus, SAD with > 270 min after sunrise are more frequent in landraces flowering in summer than in landraces flowering in winter. Our finding corroborates some earlier reports [9,13], but does not agree with some other studies [7,12] reporting FOT occurring earlier than 0800 h.

3.2 The relationships between FOT and FED

It appears that FED is inversely related to FOTd (FOT, expressed in a decimal hour) for both winters ($p < 0.05$) and summers ($p < 0.0001$) flowering (**Figure 3**). FOTd and SAD seem to strongly induce the shortening of FED on both cloudy and sunny days in both summer and winter (**Figure 4A**). The inverse relationship of FED with both SAD (**Figure 4A**) and with FOT (**Figure 3**) is warranted by the tight direct relationship of FOT and SAD during winter as well as summer, on both sunny and cloudy days (**Figure 3B**). This strong relationship between FOTd and SAD entails that longer SAD strictly corresponds to later FOT. As the FOT hour is always coterminous with the length of SAD, an association of FOTd with any other parameter is *ipso facto* coterminous with that of SAD.

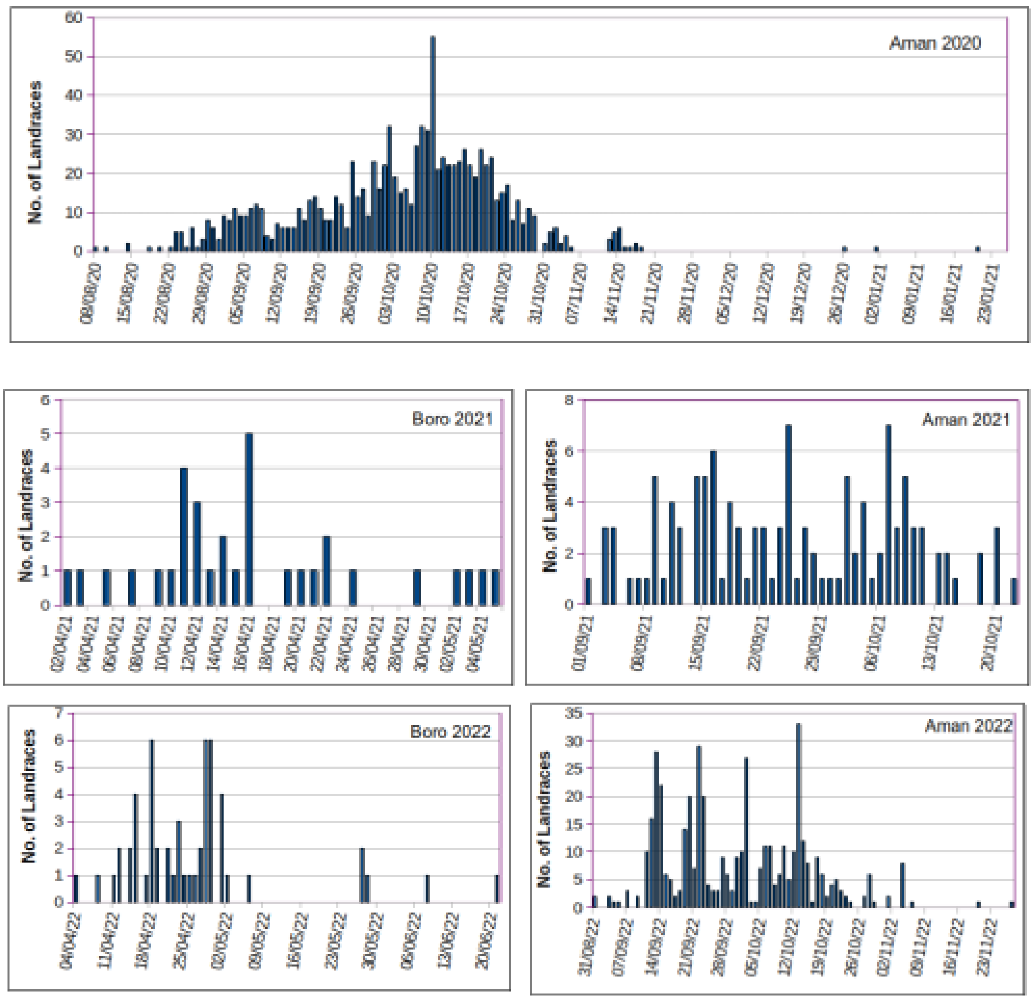

Figure 1. Frequency distribution of FOT of landraces flowering in *aman* and *boro* seasons from 2020 to 2022.

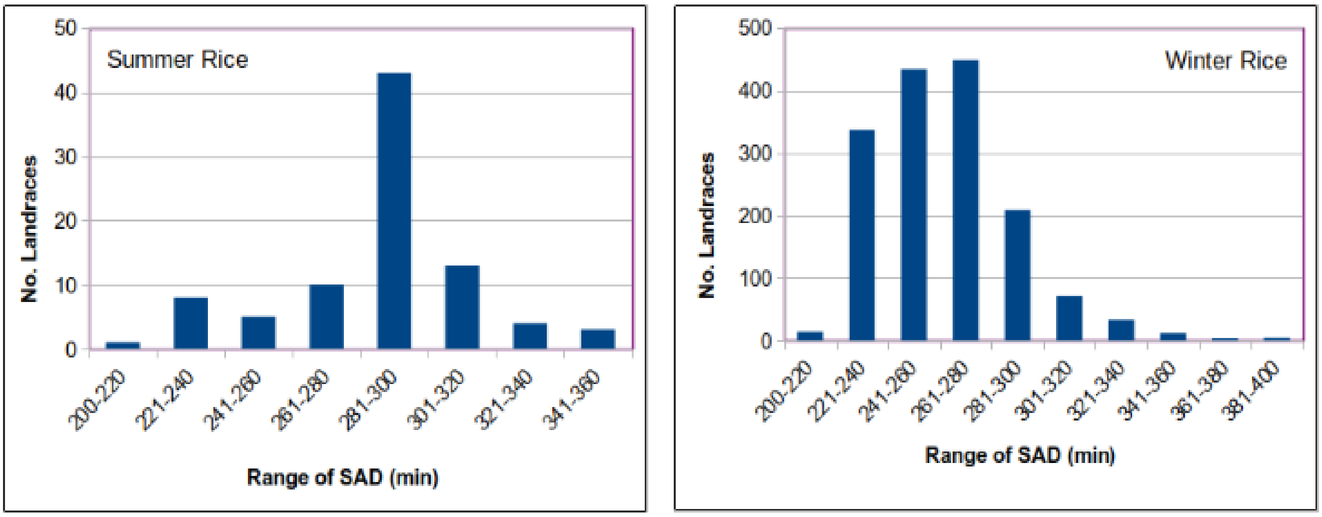

Figure 2. Frequency distribution of SAD of landraces flowering during winter and summer from 2020 to 2022 (combined).

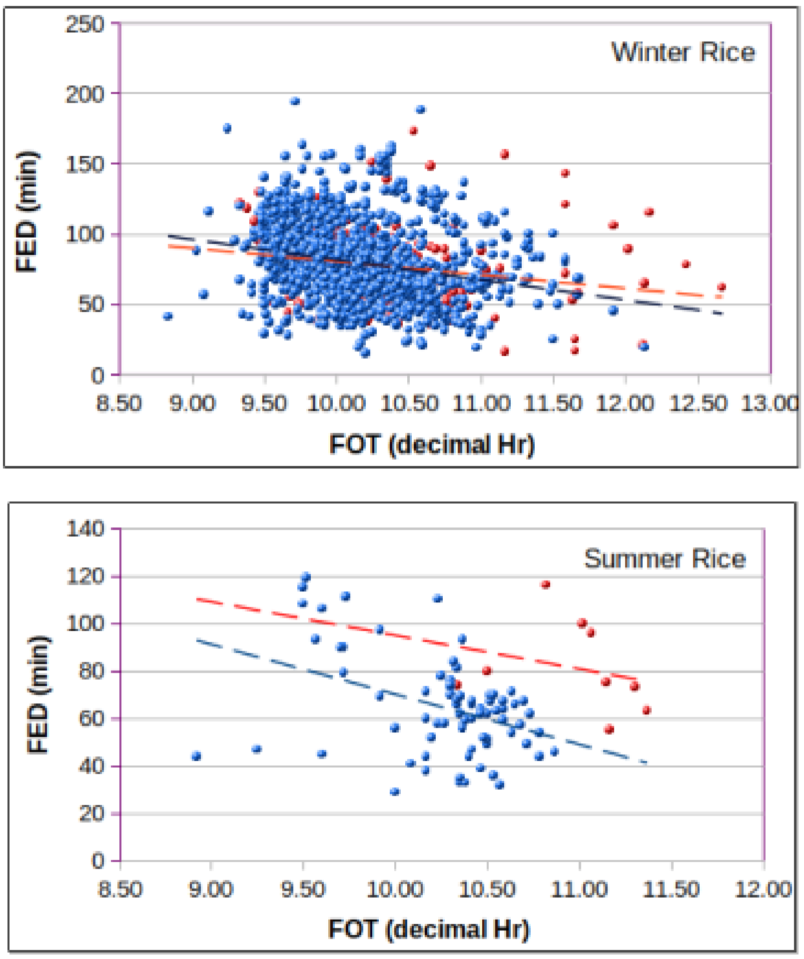

Figure 3. Regression of FED on FOT in decimal time (FOTd) for winter landraces (top panel) on sunny (blue) and cloudy days (red), with regression slope $b = -13.16$ ($R^2 = 0.051$) and -8.87 ($R^2 = 0.04$), respectively, and for summer landraces (bottom) on sunny (blue) and cloudy days (red), with regression slope $b = -21.02$ ($R^2 = 0.156$) and -14.09 ($R^2 = 0.067$), respectively.

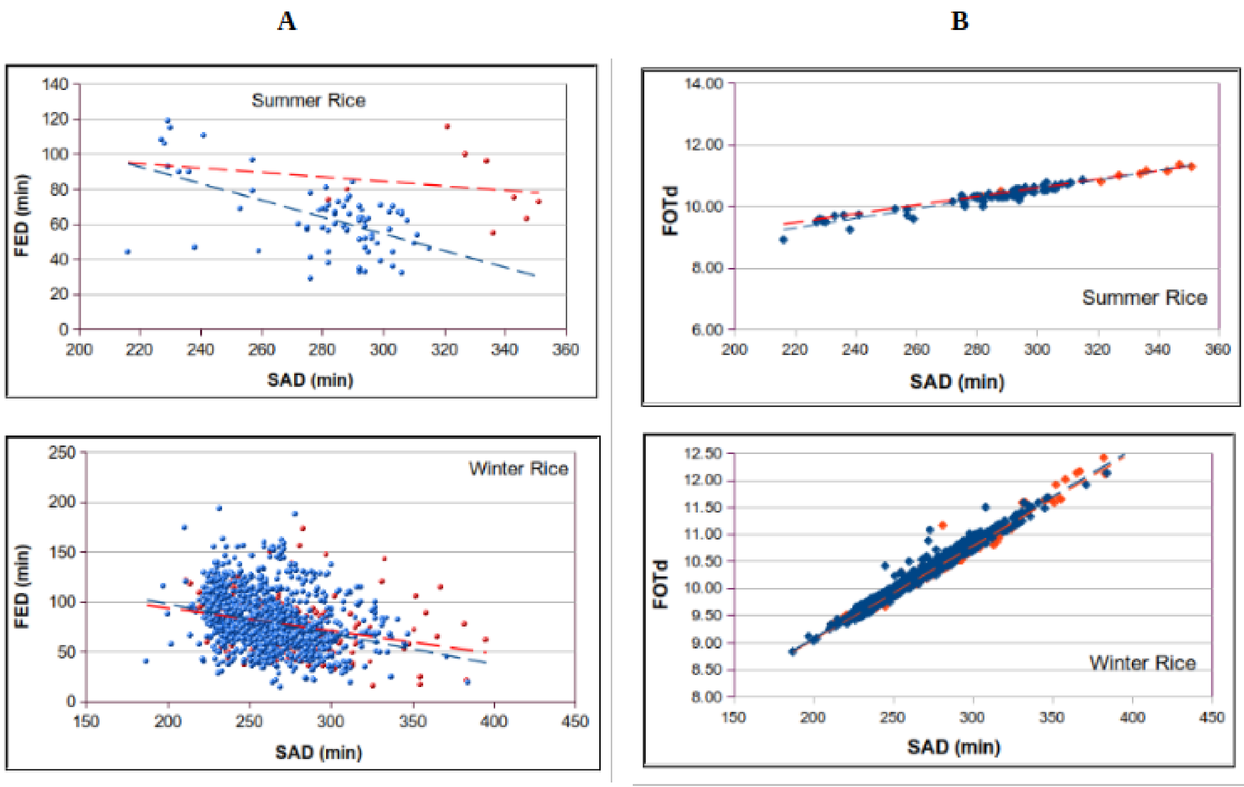

Figure 4. (A) Regression of (A) FED on SAD of summer rice landraces (top panel) on sunny (blue) and cloudy days (red), with regression slope b = –0.48 (R^2 = 0.304) and –0.127 (R^2 = 0.027), respectively, and of winter rice landraces (bottom panel) on sunny (blue) and cloudy days (red), with regression slope b = –0.303 (R^2 = 0.086) and –0.202 (R^2 = 0.066), respectively. (B) Regression of FOT (decimal hr) on SAD in summer (top) on sunny (blue) and cloudy days, with slope b = 0.02 (R^2 = 0.904) and 0.01 (R^2 = 0.97), respectively, and of winter rice landraces (bottom) on sunny (blue) and cloudy days (red), with slope b = 0.02 (R^2 = 0.97) and 0.02 (R^2 = 0.97), respectively.

3.3 The relationship of local sunrise time with FOT, FED and SAD

Several landraces opened their first florets on the same day and at about the same FOT. During colder months of *aman* season, the FOT is directly related to the sunrise time (p < 0.00001) on both sunny and cloudy days. In contrast, an earlier FOT and shorter SAD correspond to both early and late sunrise time on sunny days during summer. This is shown by a strong non-linear relationship during summer, best described by a second degree polynomial, on sunny days (**Figures 5A and 5B**), for which the adjusted R^2 was much greater than R^2 of linear regression. On cloudy summer days, the slope of regression for FOT was scarcely different from zero, while the SAD was strongly inversely related to sunrise hour during summer (that is, lengthens with receding sunrise hours). However, during short day colder seasons, SAD becomes directly related to sunrise hours, for both sunny and cloudy days (**Figure 5B**), repeating the pattern observed for the regression of FOT on sunrise hour (**Figure 5A**).

3.4 The influence of seasons on the FOT, FED and SAD of the same landraces

As the length of daylight hours changes with seasons, the FOT of a landrace is expected to change with seasonality. We compared the FOT of a total of 84 landraces, which were repeat-sown in both summer and winter over different years. The range of difference in time between FOT during summer and that between winter was 0 to 84 min, with a mean of 27.8 minutes (**Figure 6**). The difference between FOT during summer and winter was < 20 min in

55% of these landraces, while the difference was < 10 min for only 20 (= 24%) landraces.

A comparison of FOTd of the 84 landraces between *aman* and *boro* seasons from 2020 to 2022 (including the repeats mentioned in **Table 4**) reveals that the range of FOT is much wider during winter than during summer (**Figure 7A**), and that FOT tends to be delayed (**Figure 7B**), and correspondingly, SAD tends to lengthen (**Figure 8B**) when the sun rises progressively earlier in hotter months until Summer Solstice. Because the distributions of the FOTd, FED and SAD during both *Aman* and *Boro* seasons do not support the assumption of normality (**Table 5**), we conducted Mann-Whitney *U* test, instead of *t*-test for the difference between the means of FOTd during winter and summer. In general, rice florets tend to open later on hot summer days than during winter: The difference between means of the FOTd in two seasons (**Figure 7A**) was highly significant (Mann-Whitney $U = 1726.5$, $z = 5.71$, $p < 0.0001$), the difference being predominantly caused by delayed FOT during summer in over 70% of the same landraces (**Figure 7B**).

In 81% of the same landraces grown in both seasons, the mean SAD was significantly (Mann-Whitney $U = 1165.5$, $z = 7.49$, $p < 0.00001$) longer during summer than during winter (**Figure 8B**). Conversely, the FED was significantly (Mann-Whitney $U = 2267.5$, $z = 3.997$, $p < 0.0001$) longer during winter than during summer in 70% of these same landraces (**Figure 8A**). This mutually contrary seasonal effect on FED and SAD is consonant with the strong inverse relationship between FED and SAD (**Figure 4**).

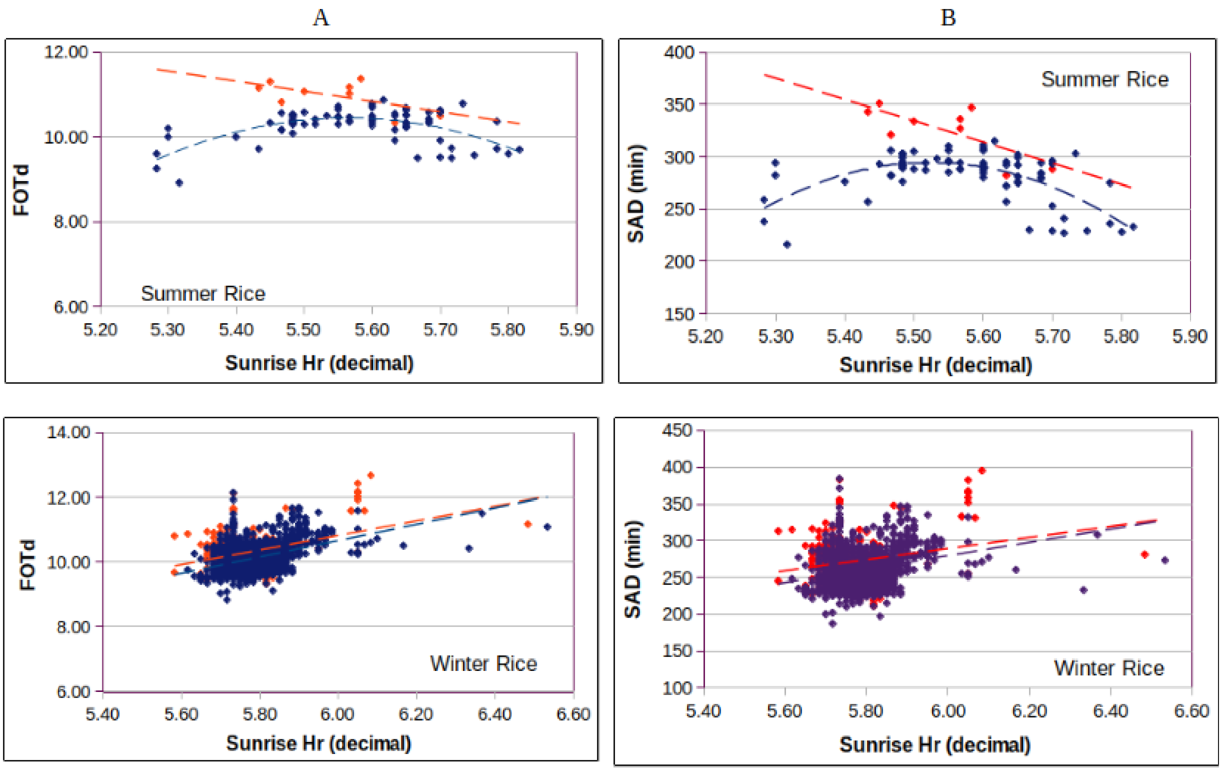

Figure 5. (A) Relationship of FOT (decimal hr) with local sunrise time in summer (top panel) on sunny days (blue), with second degree polynomial (*adjusted* $R^2 = 0.40$), and on cloudy days (red), with linear slope $b = –2.38$ ($R^2 = 0.36$), respectively; and of winter landraces (bottom) on sunny (blue) and cloudy days (red), with regression slope $b = 2.53$ ($R^2 = 0.18$) and $b = 2.26$ ($R^2 = 0.14$), respectively. (B) Relationship of SAD with sunrise time (decimal hr) in summer (top panel) on sunny days (blue) with second degree polynomial slope (*adjusted* $R^2 = 0.41$) and on cloudy days (red), with linear regression slope $b = –203.1$ ($R^2 = 0.53$), respectively; and in winter (bottom) on sunny (Blue) and cloudy days (red), with regression slope $b = 91.62$ ($R^2 = 0.07$) and $b = 75.84$ ($R^2 = 0.05$), respectively.

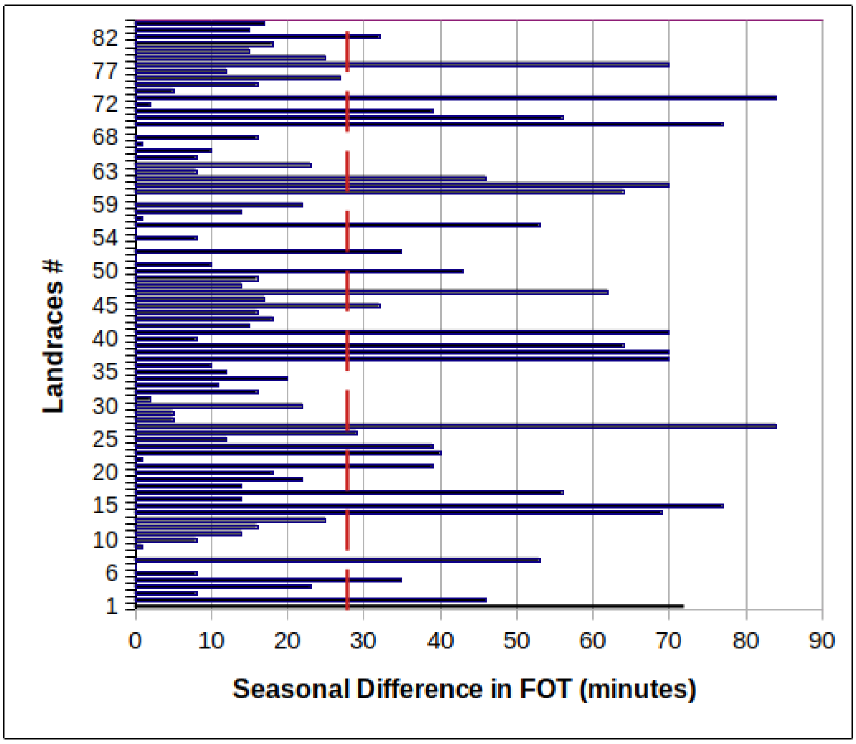

Figure 6. The difference of FOTs (in minutes) of 84 landraces between *Boro* and *Aman* seasons in different years. The red broken line is the mean difference.

Table 5. Test of normality of distribution of FOTd, FED and SAD of 84 landraces grown during two seasons.

	Shapiro-Francia W'	*p*	Anderson-Darling W	*p*
FOTd *Aman*	0.0394	0	1.0063	0.0112
FOTd *Boro*	0.0194	0	0.6485	0.0876
FED *Aman*	0.0099	0	0.9294	0.0175
FED *Boro*	0.0030	0	2.2225	0.00001
SAD *Aman*	0.0307	0	0.9407	0.01642
SAD *Boro*	0.0026	0	0.9167	0.0188

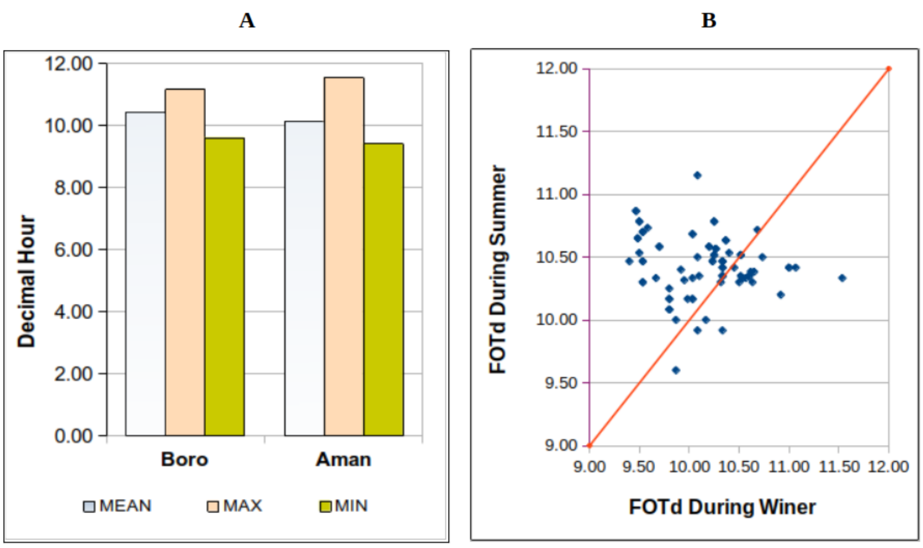

Figure 7. (A) The range and mean of FOTd of 84 landraces flowering during boro and aman seasons. (B) A comparison of FOTd of the same landraces flowering during winter and summer from 2020 to 2022; the red line is the isocline.

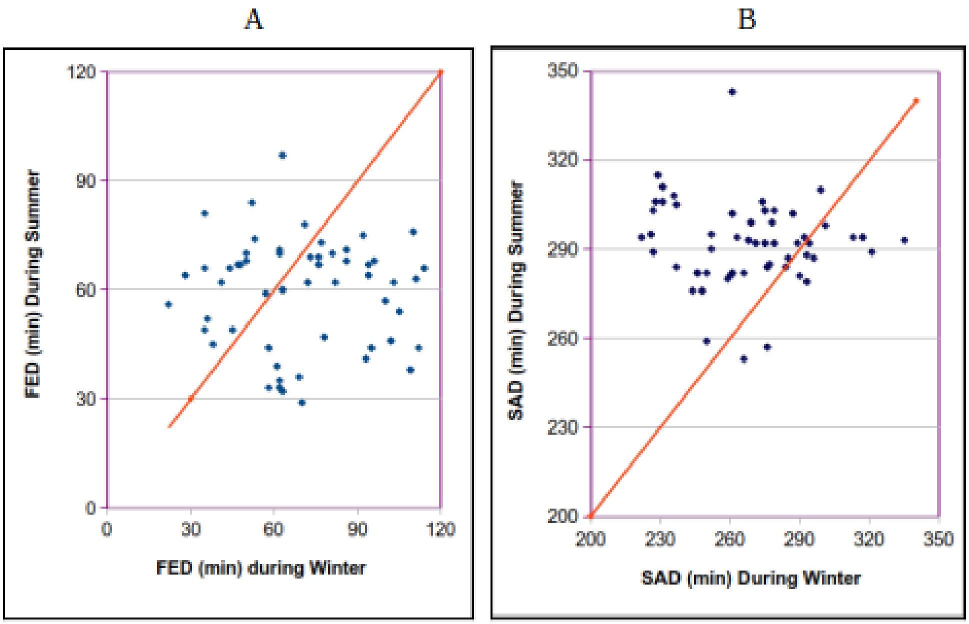

Figure 8. A comparison of (A) FED and of (B) SAD of 84 landraces flowering during winter and summer from 2020 to 2022. The red line in each panel is the isocline. Two-tailed t = 4.97 for FED and 8.005 for SAD.

4. Conclusions

Our observations of SAD and FED during summer and winter may be summarized as follows:

(a) None of the landraces examined here opens their florets earlier than 0850 h; the FOT delays on cloudy/rainy days.

(b) The SAD of *O. sativa* ssp. *indica* landraces tend to lengthen when the sun rises earlier during summer.

(c) The flowers that open late in the morning on sunny days tend to close quicker.

(d) The FED tends to shorten with longer SAD, both during summer and winter; this shortening is more prominent during summer than during winter, presumably to protect the pollen from higher midday temperatures.

(e) As the sun rises later in the morning during winter, the florets tend to open progressively earlier, and remain open longer during winter likely in wait for a longer exposure to sunlight.

As conventional farmers, as well as breeders, often may grow several cultivars on neighbouring plots on the presumption of very low cross pollination chances, a wide window of FED and a wide range of overlap between FOT and FED of the neighbouring cultivars may result in a high frequency of cross pollination. This is of crucial importance for the genetic purity of landraces with special morphological and agronomic traits. As long as the neighbouring pairs have a considerable overlap of FOT and FED, high cross pollination frequencies are likely to be more prevalent in cultivated rice than so far reported in the literature (Moldenhauer and Gibbons 2003; OGTR 2005). In contrast, a wide (> 2 hours) temporal gap between the FOTs of the neighbouring cultivars may obviate cross pollination. It would thus be necessary to take note of the extent of FOD and FED overlaps between neighbouring cultivars on the farm during different growing seasons, in order to preclude the chances of cross pollination and maintain germline purity of each of the neighbouring landraces, as well as to ensure cross pollination success in hybridization experiments.

Author Contributions

DD conceived, designed, and supervised the study, analysed the data, and prepared the mss. DB, MN and RG recorded all the data pertaining to anthesis behavior of 1114 landraces *in situ*. NVJ supervised all statistical analyses and edited the mss.

Conflict of Interest

Authors declare no competing interests.

Data Availability Statement

The primary data of FOT and FED of all rice landraces, as well as air temperature and sunrise data are freely available on Harvard Dataverse (Deb 2022). All other data will be freely available on request.

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