Botanical Studies in the Genus *Oryza*

V. Flowering Time

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Flowering order in the *Oryza* species was reported by KATAYAMA (6). In the report, seventy six strains belonging to 24 species of the genus *Oryza* were used. The flowering of spikelets in a panicle takes place in a regular sequence. In rachis level, flowering starts from the uppermost rachis of a panicle and proceeds to the lowest rachis in succession in all species used. But in rachilla level, the pattern of flowering order was divided into three groups in accordance with the flowering order.

Flowering time was reported in *Oryza sativa* (1), in the genus *Triticum* (2), *Triticum aestivum* L., *Secale cereale* L., *Avena sativa* L., *Panicum miliaceum* L. (7) and others. Flowering time in the *Oryza* species was preliminary reported by KATAYAMA (3 and 4). Flowering time of *Gramineae* species is a complex physiological phenomenon as shown by many reports mentioned above. It is determined by a number of internal and external factors, such as temperature, water content, relative humidity, light intensity and others.

Informations of flowering order and time are of great use for botanical studies and plant breeding. Especially in *Oryza*, a spikelet is available for fertilization centering around flowering day, and a pollen is available for fertilization only for a few minutes, especially in the case of wild species. The detection of the flowering time of the available spikelet in the respective day for the breeding is requested seriously. Then, using *Oryza* species for the present experiments, the writer studied the flowering time in detail.

Materials and Method

Seventy six strains belonging to 24 species of the genus *Oryza*, including 2 cultivated and 22 wild species, were used in the present investigation.

Enumerations of the species, their distribution and chromosome numbers were given in Table 1 of the previous paper (5). The plants were grown in the greenhouse of National Institute of Genetics, Misima, Shizuoka (35°09'N, 138°55'E). When lemma and palea of each spikelet were occasioned to be separated from each other, the spikelet was considered to be flowering in this experiment. One to six strains, originated from different localities, of each species were used. The observations were made 25 days during September 5 to November 18, 75 days. In

Table 1. Time of flowering start of each

Month	Sept.	Sept.	Sept.	Sept.	Oct.	Oct.	Oct.	Oct.	Oct.	Oct.
Date	5	12	23	29	3	4	6	10	15	19
Sunrise	518*	522	531	536	538	539	541	544	548	550
Sunset	1810	1759	1741	1732	1726	1725	1721	1716	1710	1705
Civil twilight	26	26	26	26	26	26	26	26	26	26
O. sativa		655	700	650	745	750	800	740	745	800
O. sativa var. *spontanea*				650	750	800	800	750	800	810
O. perennis					800	810	815	800	810	815
O. glaberrima			750	750	750	800	800	755	815	755
O. stapfii					600			635		
O. breviligulata					910	1000	920	850	900	910
O. officinalis	600			600	605		530		740	
O. minuta	600		540	605	650	640	700	640	750	
O. malabarensis					640		620	635		
O. malampuzhaensis				635		625	620	630	640	
O. eichingeri	600		600		632		635			630
O. punctata			550	620	620	615		710	710	655
O. latifolia	700		525	600			505		535	540
O. alta			400	540	430		400		430	
O. grandiglumis					510		530		535	
O. australiensis		1640	1700		1710	1630	1620		1400	1700
O. meyeriana subsp. *granulata*	400		500	430	500		415		400	
O. meyeriana subsp. *meyeriana*		400	500	420	450	455		450	400	
O. meyeriana subsp. *abromeitiana*			420		500	415	410			415
O. ridleyi					490			400	420	430
O. longiglumis				410	420	440	430		440	500
O. coarctata					1710	1720	1720		1700	1600
O. brachyantha		1000		950	1000			1000	950	
O. tisseranti	950		1000			1000		950		940
O. perrieri		1000	1020		1000		950		1000	1000
O. subulata	600		610	550	615		650		605	

* 5 o'clock and 18 minutes

species from September 5 to November 18 .

Oct.	Oct.	Oct.	Oct.	Oct.	Oct.	Nov.	Nov.	Nov.	Nov.	Nov.	Nov.	Nov.	Nov.	Nov.
20	23	24	26	27	31	2	3	4	5	11	12	13	16	18
551	554	555	556	557	601	603	604	606	607	614	615	616	618	621
1704	1700	1659	1656	1655	1651	1650	1650	1648	1646	1643	1642	1641	1638	1637
26	26	26	27	27	27	27	27	27	28	28	28	28	28	28
735	800	840	910	935	850		850	900	920	930	1100	1050	1040	1030
820	810	815	935	915		900	845		915	920		1040	1050	1045
800	820	840	930	930	940	950		940		1000	1000	950	955	
820	825	815	915	925	905	915		940	930		1000		1000	
700			705		715	730	710		700	635	725	820		740
	925		940	930	630	730	750		625	830	830	940	1000	
440		550	610	705			645	630	710	610	705		605	610
550	620	610		800		635	640	640	800	600	550			
700	710			700		640	620	635		630			635	620
705	715	640		635	620		640		630		625		645	
625	650	650	645		700	655	720	740	715	950	1030		1025	
700	700	650	710	700	640	735			720	830	755		940	955
525		545	545		515		545	700	620	600	530		620	
425	515	510	435		510		500	540	600	530	530		540	600
540			535		600	620	520	515	555		545		550	530
1620	1700		1400	1540		1545	1600		1430		1405	1630	1700	
425		450	415		400	410	415	400	400	430	400		400	400
	410	420		430		410	405		400		400		400	
420		500	400	400			410	405	415		405		405	405
500		440	450		400		420		800	635	500		450	545
	450		445	520		500		620	755		540		450	700
	1610		1540	1500		1500	1500	1425	1200		1340	1400	1335	1340
	1000	1000	930	940	950	1000	1000	1000	1100	945	1020		1000	
	1000			1000		1000	1000	950	1050			1050	1100	1100
	1000	1000	950		1000		950	1000		1000		950		1100
610		555			517		600		730	600	530		550	610

the preliminary studies, as no obvious intraspecific variation in flowering time was recognized in each species, one strain of each species was used in this experiment. *O. barthii* was omitted because of its irregular flowering behaviour.

Results and Discussion

Flowering time in the respective day was recorded when lemma and palea of the first spikelet in a panicle opened. The duration of flowering time is the interval between opening and closing of the flowering glumes in the respective day.

Observations on the average flowering time are given in Table 1 and Figs. 1 to 26. Date, sunrise, sunset, civil twilight in the morning as well as in the evening by minute and flowering time of each species in the respective day are shown in Table 1. In the Table 1, the species are arranged in taxonomical order. In Figs. 1 to 26, the observed relation between the flowering time and days observed is shown. A numeral in vertical axis shows the o'clock in the figures.

The species name, time between the earliest and latest, and their number of days observed are shown in Table 2. In the Table 2, the earliest and latest time of the flowering start, which were recorded during the observations, between them and period of observation in number of the days are shown.

Flowering time of *O. sativa*, *O. sativa* var. *spontanea*, *O. perennis* and *O. glaberrima* are not different from one another and flowered in the morning. But *O. stapfii* and *O. breviligulata*, two wild relatives of *O. glaberrima*, flowered differently from *O. glaberrima*. Fifteen wild species, *i.e.*, *O. officinalis*, *O. minuta*, *O. malabarensis*, *O. malampuzhaensis*, *O. eichingeri*, *O. punctata*, *O. latifolia*, *O. alta*, *O. grandiglumis*, *O. meyeriana* subsp. *granulata*, *O. meyeriana* subsp. *meyeriana*, *O. meyeriana* subsp. *abromeitiana*, *O. ridleyi*, *O. longiglumis* and *O. subulata*, flowered earlier in the morning than the cultivated species and their closely related wild species. Three wild species, *i.e.*, *O. brachyantha*, *O. tisseranti*, *O. perrieri*, flowered later in the morning and two wild species, *i.e.*, *O. australiensis* and *O. coarctata*, flowered in the late afternoon.

The results indicated that flowering times are very similar in taxonomically related species with each other. Then, accordingly the present materials are divided into thirteen groups as follows: 1) *O. sativa* (Fig. 1) and *O. sativa* var. *spontanea* (Fig. 4), 2) *O. perennis* (Fig. 24), *O. glaberrima* (Fig. 3) and *O. stapfii* (Fig. 9), 3) *O. breviligulata* (Fig. 8), 4) *O. officinalis* (Fig. 20) and *O. minuta* (Fig. 7), 5) *O. malabarensis* (Fig. 26) and *O. malampuzhaensis* (Fig. 19), 6) *O. eichingeri* (Fig. 10) and *O. punctata* (Fig. 17), 7) *O. latifolia* (Fig. 6), *O. alta* (Fig. 2) and *O. grandiglumis* (Fig. 13), 8) *O. australiensis* (Fig. 16), 9) *O. meyeriana* subsp. *granulata* (Fig. 5), *O. meyeriana* subsp. *meyeriana* (Fig. 14) and *O. meyeriana* subsp. *abromeitiana* (Fig. 18), 10) *O. ridleyi* (Fig. 12) and *O. longiglumis* (Fig. 23), 11) *O. coarctata* (Fig. 25), 12) *O. brachyantha* (Fig. 15), *O. tisseranti* (Fig. 21) and *O. perrieri* (Fig. 11), 13) *O. subulata* (Fig. 22).

Correlation coefficient of the time of the flowering start on the respective days observed and linear regression between them are calculated and shown in Table 3. Sunrise, sunset and duration of civil twilight are shown in Fig.27. Eight species, *i.e.*, *O. sativa*, *O. sativa* var. *spontanea*, *O. perennis*, *O. glaberrima*, *O. eichingeri*, *O. punctata*, *O. alta* and *O. coarctata*, showed very high correlation among them at 0.1% level. Two species, *i.e.*, *O. stapfii* and *O. tisseranti*, showed low correlation coefficients at 5% level. Other 16 species showed no statistically significant correlation. The time of flowering start of nine species of the former ten species are gradually

Table 2. The species name, times between the earliest and the latest of flowering start and period of observations.

Species	Earliest time	Latest time	Difference between earliest and latest time	Period of observations
O. sativa	$6^{o}\ 50^{m}$	$11^{o}\ 00^{m}$	$4^{h}10^{m}$	68days
O. sativa var. *spontanea*	6 50	10 50	4 00	51
O. perennis	8 00	10 00	2 00	45
O. glaberrima	7 50	10 00	2 10	55
O. stapfii	6 00	8 20	2 20	47
O. breviligulata	6 25	10 00	3 35	45
O. officinalis	4 40	7 40	3 00	74
O. minuta	5 40	8 00	2 20	69
O. malabarensis	6 20	7 10	50	47
O. malampuzhaensis	6 20	7 15	55	49
O. eichingeri	6 00	10 30	4 30	72
O. punctata	5 50	9 55	4 05	57
O. latifolia	5 05	7 00	1 55	72
O. alta	4 00	6 00	2 00	57
O. grandiglumis	5 10	6 20	1 10	47
O. australiensis	14 00	17 10	3 10	66
O. meyeriana subsp. *granulata*	4 00	5 00	1 00	74
O. meyeriana subsp. *meyeriana*	4 00	5 00	1 00	66
O. meyeriana subsp. *abromeitiana*	4 00	5 00	1 00	57
O. ridleyi	4 00	8 00	4 00	47
O. longiglumis	4 10	7 55	3 45	51
O. coarctata	12 00	17 20	5 20	47
O. brachyantha	9 30	11 00	1 30	66
O. tisseranti	9 40	11 00	1 20	74
O. perrieri	9 50	11 00	1 10	68
O. subulata	5 17	7 30	2 13	74

delayed from September to November. The time of flowering start of one species of the former ten species, *i.e.*, *O. coarctata*, is gradually accelerated from September to November. Flowering time of the nine species seems to be controlled by sunrises, because sunrise becomes gradually to later from September to November. That of *O. coarctata* seems to be controlled mainly by the temperature, because temperature becomes gradually lower in the afternoon from September to November. In fact, a plant of the species, which showed statistically significant correlation coefficient, is easily to be controlled in its flowering start by artificial treatment. Practically at the crossing experiment, a plant of such species is delayed in the flowering start by the artificial dark treatment. It is very useful for plant breeding.

Linear regression of the time of flowering start on the respective days observed in *O. sativa*,

Table 3. Correlation coefficient and linear regression of time of flowering start (y, 1 unit = 10 minutes) on the days observed (x, 1 unit = 4 days); the origin of the x corresponds to September 5.

Species	Correlation coefficient	d. f.	Linear regression	0 point y	0 point x
O. sativa	0.907***	21	1.455x - 3.254	8^{o} 50^{m}	41
O. sativa var. *spontanea*	0.927***	17	1.510x - 0.889	8 50	48
O. perennis	0.930***	16	1.292x - 1.149	9 00	48
O. glaberrima	0.910***	17	1.100x - 0.853	8 50	46
O. stapfii	0.703*	10	0.646x - 0.646	7 10	52
O. breviligulata	-0.289	15	-0.501x+3.971	8 10	48
O. officinalis	0.235	14	0.202x+0.731	6 10	37
O. minuta	0.161	16	0.149x - 1.697	6 50	33
O. malabarensis	-0.205	10	-0.078x+0.013	6 40	52
O. malampuzhaensis	0.107	12	0.048x - 0.990	6 50	48
O. eichingeri	0.738***	15	1.303x - 9.321	8 10	37
O. punctata	0.918***	17	1.428x - 5.429	8 00	46
O. latifolia	-0.289	14	-0.231x - 1.271	6 00	37
O. alta	0.750***	15	0.634x - 0.134	5 00	46
O. grandiglumis	0.476	11	0.281x - 0.304	5 40	52
O. australiensis	-0.347	15	-0.508x+2.195	15 30	40
O. meyeriana subsp. *granulata*	-0.398	16	-0.162x - 1.617	4 30	37
O. meyeriana subsp. *meyeriana*	-0.471	13	-0.198x - 1.078	4 30	40
O. meyeriana subsp. *abromeitiana*	0.083	13	0.035x - 1.170	4 30	46
O. ridleyi	0.528	12	0.936x - 6.200	6 00	52
O. longiglumis	0.415	13	0.593x - 4.889	6 00	48
O. coarctata	-0.982***	14	-2.123x+2.913	14 40	52
O. brachyantha	0.186	15	0.078x - 1.133	10 10	40
O. tisseranti	0.688*	12	0.388x - 1.922	10 20	37
O. perrieri	0.211	13	0.078x - 1.863	10 20	40
O. subulata	- 0.123	13	-0.067x - 1.424	6 20	37

***, *: Significant at 0.1% and 5% level, respectively.

for example, is calculated as follows: $Y = 1.455\ X - 3.254$
where Y and X indicate time of the flowering start (1 unit = 10 minutes) and days observed (1 unit = 4 days), respectively. This formula indicates that the time of flowering of *O. sativa* becomes 14.55 (= 1.455×10) minutes later, during 4 days advanced. In other words, time of flowering becomes 3.64 (= $14.55 \div 4$) minutes later on one day advanced from September to November. Astronomical day lengths on September 5 and November 18 are 12 hours 52 minutes and 10 hours 16 minutes, respectively; *i.e.*, there is 2 hours and 36 minutes difference between September 5 and November 18. So, the astronomical day length becomes 2.110 (=2^{h}

$36^{m} \div 74$ days) minutes shorter per day on the average during the experiment. 0.844 (=2.110 $\times 4 \div 10$) minutes corresponds to the average minutes of decrement in astronomical day length.

Statistically significant delaying or acceleration of the flowering start was observed in 10 species. Among them, six species, *i.e.*, *O. sativa*, *O. sativa* var. *spontanea*, *O. perennis*, *O. glaberrima*, *O. eichingeri* and *O. punctata*, were ascertained to have delaying earlier than that of the astronomical day length, in which changing values (for example, *O. sativa* showing 1.455) are more than that of the astronomical day length (=0.844). A species, *i.e.*, *O. coarctata*, showed acceleration than that of astronomical day length. Three species, *i.e.*, *O. stapfii*, *O. alta* and *O. tisseranti* showed delaying smaller than that of the astronomical day length, in which changing values are smaller than that of the astronomical day length.

Some differences from average pattern of flowering start in several species are found frequently, especially on October 15, October 27, November 5 and November 12. According to the record of temperature, it seems to be owing to relatively low temperatures. It is presumable, moreover, that differences of civil twilight of natural habitat, in which wild species were growing, have some influences upon the flowering behaviour.

The species studied can be roughly classified into four groups with respect to their flowering responses to climatic conditions, which were recorded from September to November. In the first group, the flowering time is very stable regardless of the climatic conditions. *O. malabarensis*, *O. malampuzhaensis*, *O. grandiglumis*, *O. meyeriana* subsp. *granulata*, *O. meyeriana* subsp. *meyeriana*, *O. meyeriana* subsp. *abromeitiana*, *O. brachyantha*, *O. perrieri* and *O. subulata*, belong to this group. In the second group, the flowering time is labile in regard to the climatic conditions. *O. breviligulata*, *O. officinalis*, *O. minuta*, *O. latifolia*, *O. australiensis*, *O. ridleyi* and *O. longiglumis*, belong to this group. In the third group, the flowering time vary mainly with the time of sunrise, *i.e.*, it becomes gradually later from September 5 to November 18 in accordance with the calender. Yet there is a few intra-strain's variation. *O. sativa*, *O. sativa* var. *spontanea*, *O. perennis*, *O. glaberrima*, *O. stapfii*, *O. eichingeri*, *O. punctata*, *O. alta*, *O. tisseranti* belong to this group. In the fourth group, the flowering time is gradually accelerated in accordance with the fall of temperature. *O. coarctata* belongs to this group.

The relative humidity in the greenhouse was kept at more than 70%. However, relative humidity did not bring any influence upon the flowering time of *Oryza* species.

The flowering duration of five species is shown in Fig. 28. Actual number of spikelets which flowered (vertical axis) in the respective time (abscissa) is illustrated in the figure. *O. sativa* (*1* in Fig. 28) and *O. glaberrima* (*3* in Fig. 28), the cultivated species, show their peak number earlier than that of *O. sativa* var. *spontanea* (*2* in Fig. 28), *O. stapfii* (*4* in Fig. 28) and *O. officinalis* (*5* in Fig. 28). According to the data obtained from all species used, the characteristic of each species in flowering duration are not so remarkable as that of time of the flowering start. However, the following characters are clearly ascertained that the species distantly related to the cultivated species show, in general, not the same but either longer or shorter duration, and not the same but later peak of the flowering spikelets.

Because temperature, relative humidity, water condition and light intensity relations have been considered the main external limiting factors governing the flowering of plants, such differences between the changing in astronomical day length and time of flowering start of *Oryza* species will be owing to some external factors mentioned above and some internal factors. Upon such relationships, further studies will be truly requested.

Summary

Seventy six strains belonging to 24 species of the genus *Oryza* were used for investigation of flowering time.

On the time of flowering start, the species can be roughly classified into four groups with respect to their responses to climatic conditions. In the first group, the flowering time is stable in regardless of the climatic conditions; 7 species belong to this group. In the second group, the flowering time is labile in regard to the climatic conditions; 7 species belong to this group. In the third group, the flowering time vary mainly with the time of sunrise, having highly correlation coefficient between them; 9 species belong to this group. In the fourth group, the flowering time vary mainly with the temperature, having highly correlation coefficient between them; 1 species belongs to this group. Some biological significance of the flowering time was discussed.

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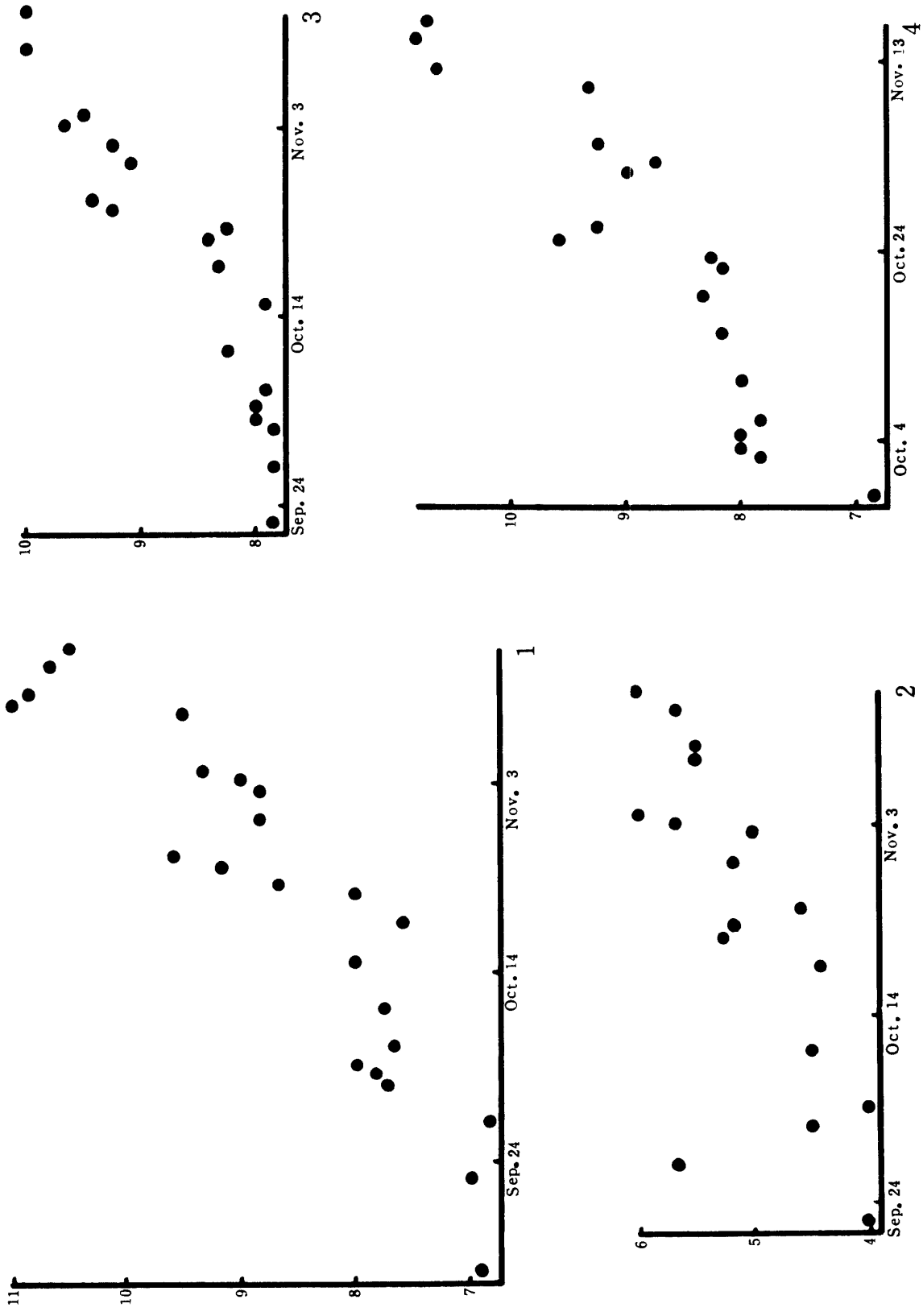
Explanation of Figures 1 to 28

Figs.1 to 26. Relation between time of flowering start and days observed. Vertical axis; time in o'clock. Abscissa; flowering date observed. Fig. 1; *O. sativa*, Fig. 2; *O. alta*, Fig. 3; *O. glaberrima*, Fig. 4; *O. sativa* var. *spontanea*, Fig. 5; *O. meyeriana* subsp. *granulata*, Fig. 6; *O. latifolia*, Fig. 7; *O. minuta*, Fig. 8; *O. breviligulata*, Fig. 9; *O. stapfii*, Fig. 10; *O. eichingeri*, Fig. 11; *O. perrieri*, Fig. 12; *O. ridleyi*, Fig. 13; *O. grandiglumis*, Fig. 14; *O. meyeriana* subsp. *meyeriana*, Fig. 15; *O. brachyantha*, Fig. 16; *O. australiensis*, Fig. 17; *O. punctata*, Fig. 18; *O. meyeriana* subsp. *abromeitiana*, Fig. 19; *O. malampuzhaensis*, Fig. 20; *O. officinalis*, Fig. 21; *O. tisseranti*, Fig. 22; *O. subulata*, Fig. 23; *O. longiglumis*, Fig. 24; *O. perennis*, Fig. 25; *O. coarctata*, Fig. 26; *O. malabarensis*.

Fig. 27. Sunrise and sunset (—), and duration of civil twilight in the morning and in the evening (- - - -).

Fig. 28. Some examples of the actual number of spikelets flowered (vertical axis) in each time from flowering start (abscissa). *1; O. sativa, 2; O. sativa* var. *spontanea, 3; O. glaberrima, 4; O. stapfii, 5; O. officinalis.*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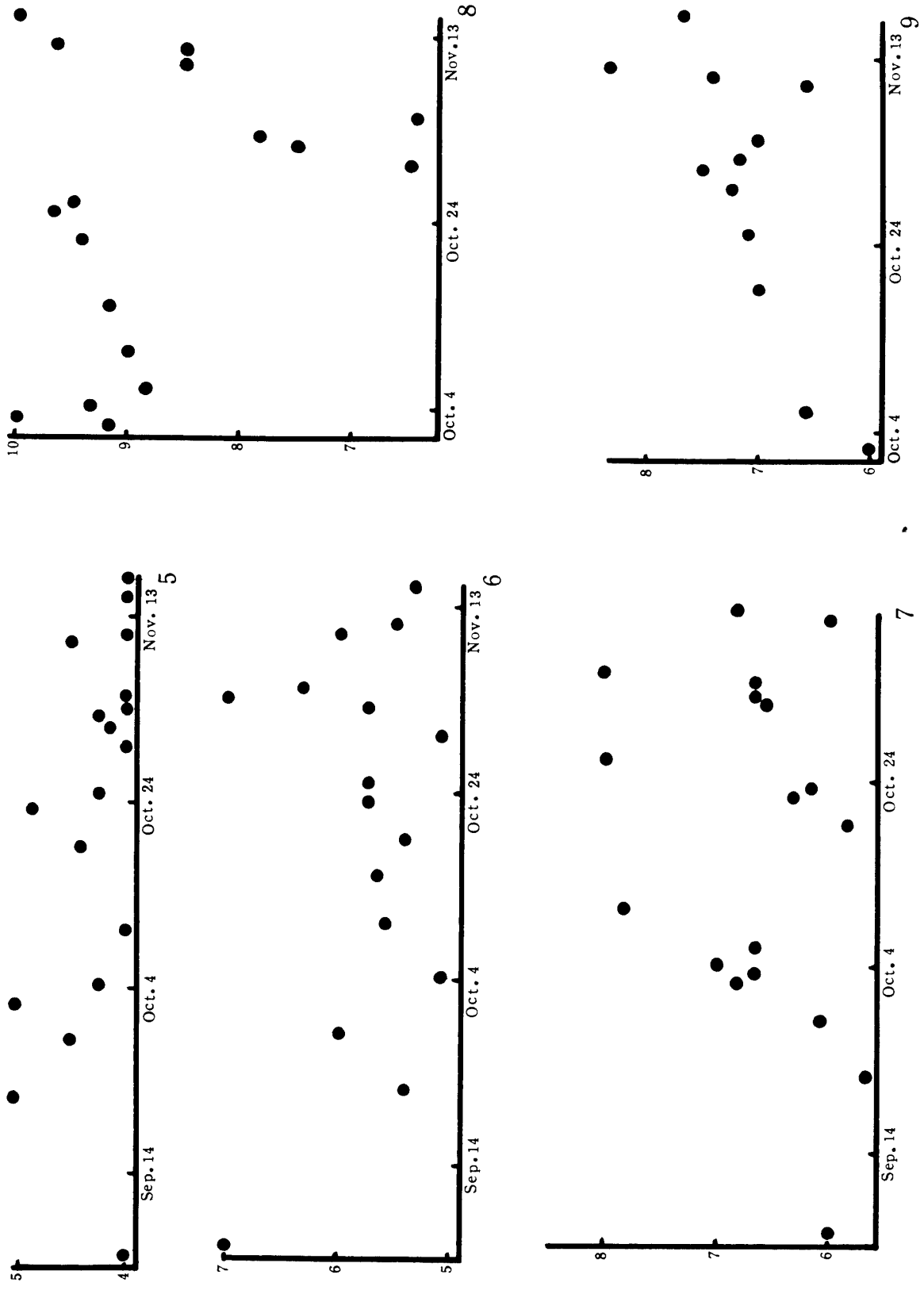
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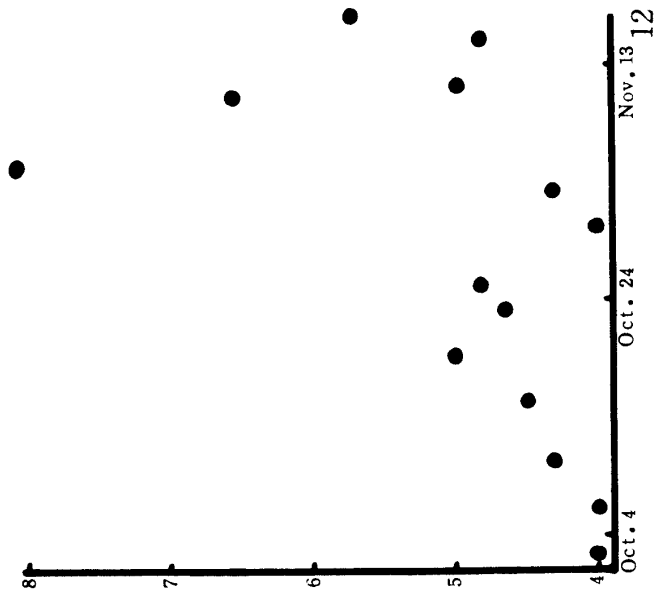
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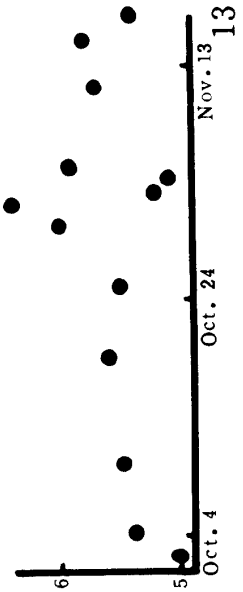
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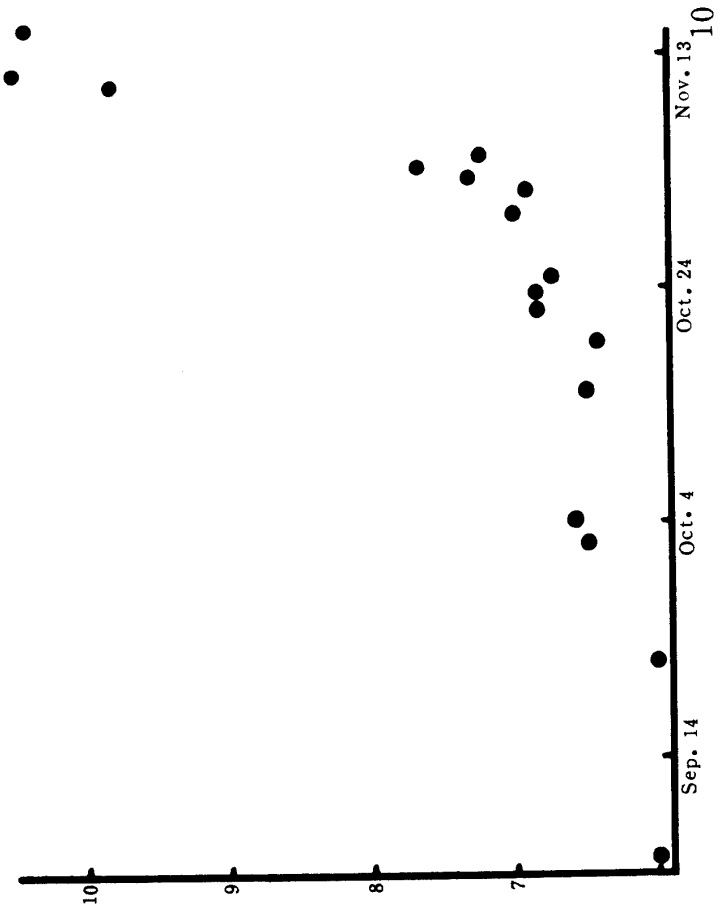
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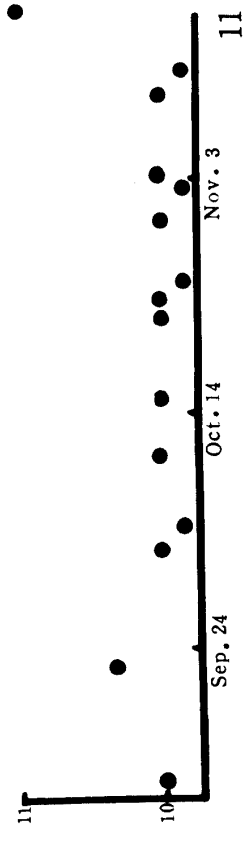
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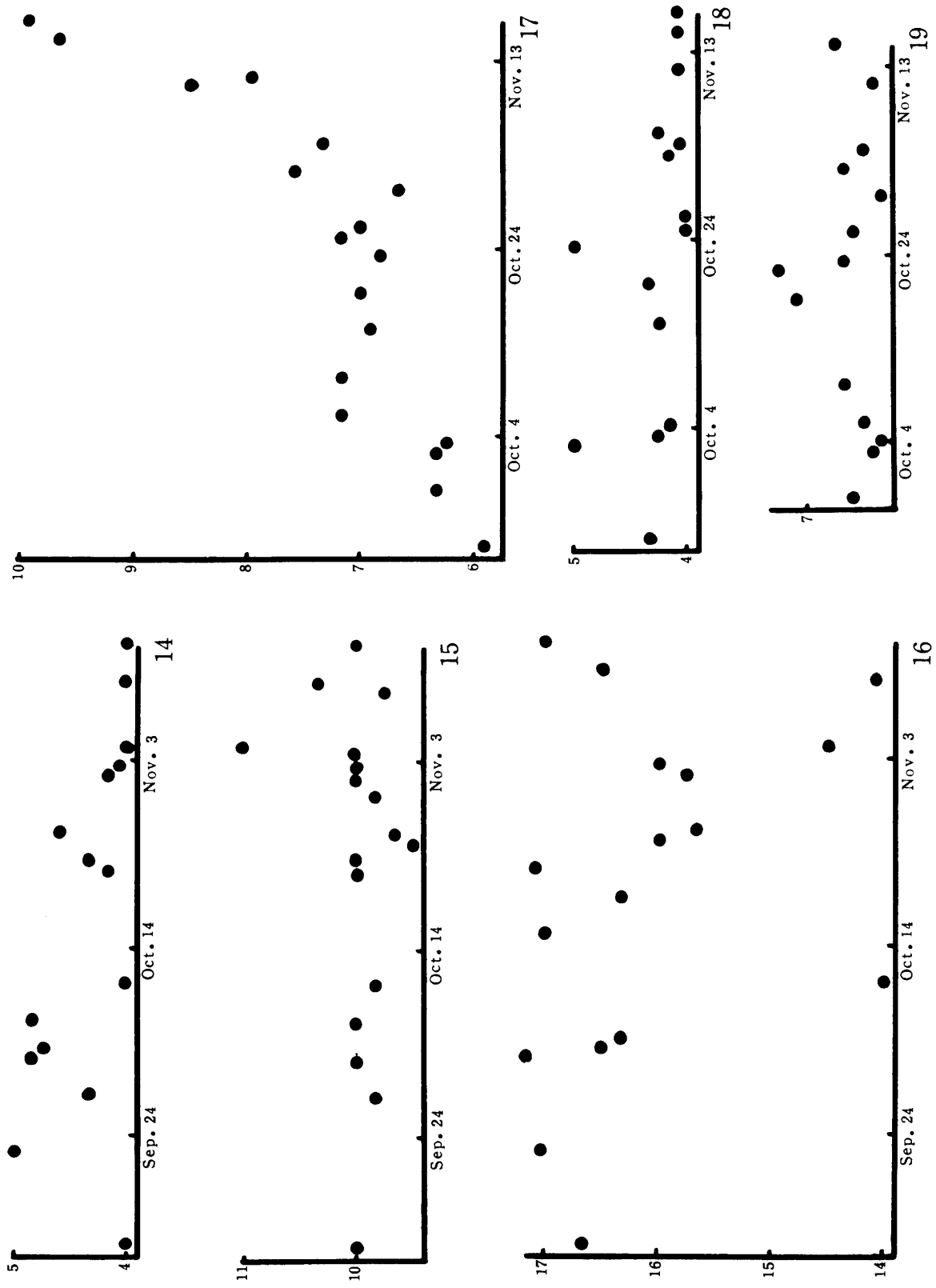
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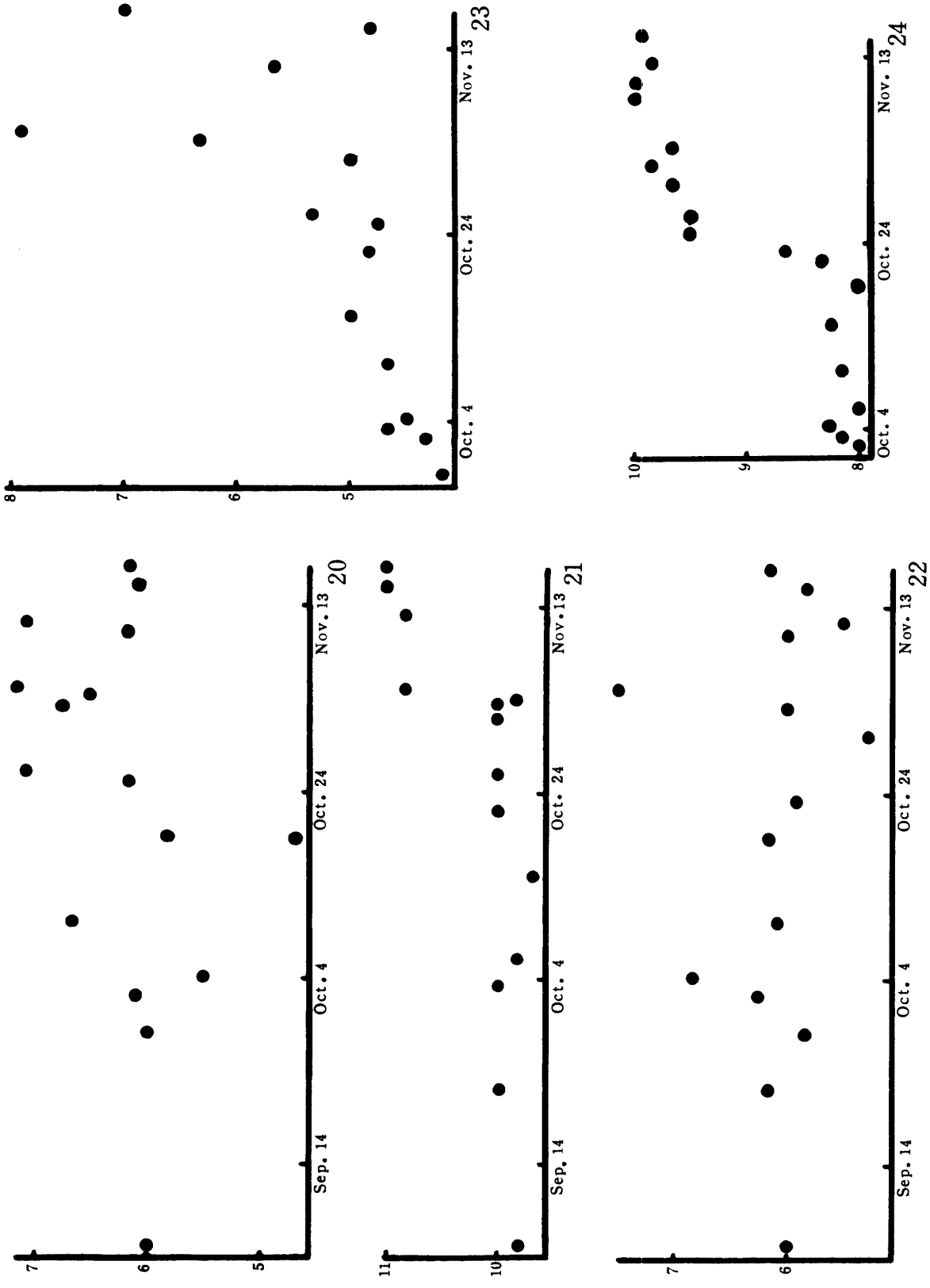
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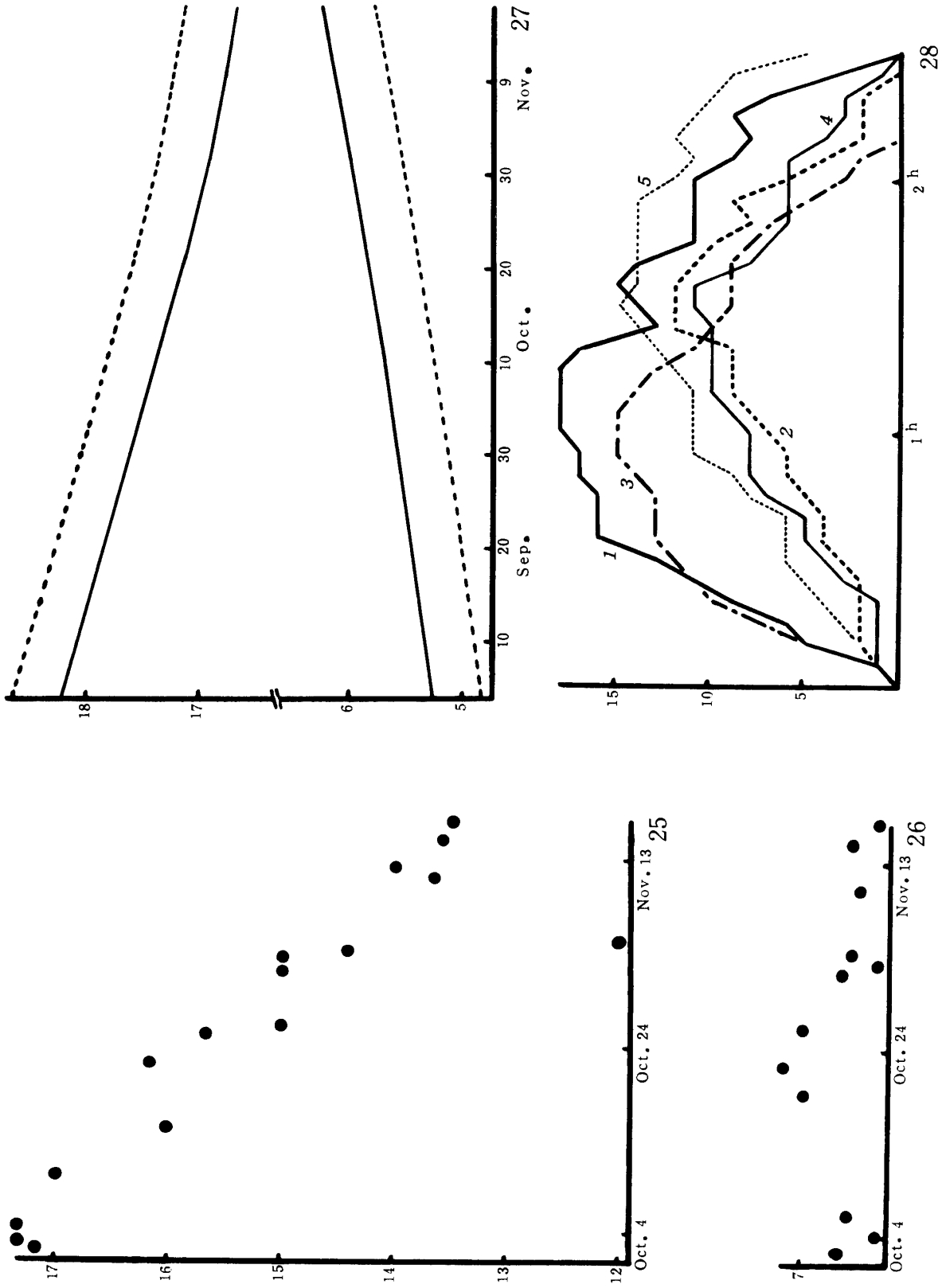
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