Theor Appl Genet (1987) 74:487–492

Monosomic analysis of heading date and spikelet number in the common wheat (*Triticum aestivum* L.) multispikelet line 'Noa'

E. Millet

Department of Plant Genetics, The Weizmann Institute of Science, Rehovot 76 100, Israel

Received January 26, 1987; Accepted February 23, 1987
Communicated by J. Mac Key

Summary. Genetic analysis of heading date and spikelet number was carried out in the common wheat (*Triticum aestivum* L.) multispikelet line 'Noa', by using the monosomic series of the regular line 'Mara'. 'Noa's' high number of spikelets was found to be controlled by a recessive major gene on chromosome 2D; a slight reduction in spikelet number was induced by another recessive gene on 'Noa's' 7A chromosome. 'Noa's' late heading date was found to be controlled by two recessive genes, located on chromosome 2D (a major effect) and 6B (a minor effect). The nature of the genes located on 'Noa's' 2D chromosome and the relationship between spikelet number and heading date are discussed.

Key words: Wheat – *T. aestivum* – Heading date – Spikelet number – Monosomic analysis

Introduction

A large number of spikelets per spike in bread wheat is commonly associated with delayed heading date (Rahman and Wilson 1977; Rawson 1971). This has been ascribed to the prolonged developmental phases involved in spikelet production or associated with it. These are (1) the vegetative phase which affects the number of spikelet primordia at the commencement of spike differentiation (Halse and Weir 1970); (2) the spikelet production phase at which spikelets are added after the transition into the reproductive phase and (3) the post-differentiation phase lasting from terminal spikelet differentiation until heading. The duration of the latter phase is correlated with those of the previous ones (Pinthus 1963).

In an attempt to produce early lines with many spikelets, the association between late heading date and large number of spikelets per spike was investigated using several bread wheat lines, including the multispikelet line 'Noa' and some of its derivatives (Millet 1983, 1986a). It was recently reported (Millet 1986b) that 'Noa' has a large initial number of spikelets per spike – not associated with a prolonged vegetative phase. It was also found that 'Noa' carries on its 2D chromosome an allele for a prolonged post-differentiation phase. This study aimed to screen 'Noa's' genome, by monosomic analysis, for those alleles which contribute to the large number of spikelets per spike, and to assess their relationships to the time of ear emergence.

Materials and methods

Seeds of the monosomic series of 'Mara' (a regular type Italian cultivar) were obtained from B. Giorgi, ENEA, Italy. They were the progeny of at least the seventh generation of backcross to 'Mara'; monosomic plants of each line were uniform. The seeds were planted in summer, 1983. Monosomic plants were selected by chromosome counts at meiosis and were pollinated by 'Noa' (a spring type, Israeli, multispikelet breeding line). Data on heading date and spikelet number were recorded and evaluated in the following analyses.

(1) F_1 monosomic analysis, 1984: on 23. 12. 83, F_1 seeds of crosses between 'Mara' (euploid and monosomic lines) and 'Noa' were planted in pots, which were randomly distributed outdoors. The growth mixture was composed of equal amounts of peat, volcanic gravel and vermiculite, to which a slow-release fertilizer was added. Of the F_1 'Mara' monosomics × 'Noa', only monosomic plants, selected cytologically at meiosis, were analysed.

(2) Monosomic analysis of 'Mara' and of F_1 hybrids ('Mara' × 'Noa'), 1985: on 3. 12. 84, five seeds of each monosomic hybrid selected in the previous season and the euploids 'Mara' and 'Noa' were planted at random in a light

Table 1. Means ± SE of spikelet number and heading date (days from seedling emergence) of main spike of 'Noa', 'Mara', the F_1 hybrid ('Mara' × 'Noa') and monosomic F_1's derived from pollination of 'Mara' monosomic series by 'Noa'. The missing chromosomes of 'Mara' in the monosomic hybrids are indicated (1984 experiment)

	Spikelet no.						Heading date					
Euploid plants												
'Noa'	28.3±0.3***						110.5±0.9***					
'Mara'	26.8±0.5***						110.0±1.0***					
F_1 ('Mara' × 'Noa')	24.7±0.3						98.8±0.4					
Monosomic F_1												
1A	24.0±0.1	1B	25.3±0.4	1D	–		1A	102.0±0.0***	1B	102.5±0.7***	1D	–
2A	24.0	2B	24.8±0.2	2D	28.5±0.5***		2A	102.0	2B	99.6±0.4	2D	111.0±0.0***
3A	24.0±0.8	3B	24.7±0.3	3D	–		3A	101.0±1.4	3B	98.3±0.9	3D	–
4A	24.7±0.3	4B	24.2±0.4	4D	–		4A	97.0±1.2	4B	99.8±0.9	4D	–
5A	23.7±0.3*	5B	24.5±0.5	5D	26.5±0.5**		5A	97.0±0.0**	5B	100.0±2.0	5D	101.3±1.0
6A	24.5±0.3	6B	25.0±0.0	6D	25.0		6A	99.0±0.9	6B	102.7±0.3***	6D	97.0
7A	22.7±0.6*	7B	–	7D	23.3±0.7		7A	97.8±1.2	7B	–	7D	96.3±0.3**

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$: all significant differences from the disomic F_1

Table 2. Means ± SE of spikelet number and heading date (days from seedling emergence) of main spikes of the lines 'Noa', 'Mara', monosomics of 'Mara' and monosomic F_1 hybrids derived from pollination of 'Mara' monosomic series by 'Noa' (1985)

Line		Euploid lines and monosomics of 'Mara'			F_1 hybrid and monosomics of F_1 ('Mara' × 'Noa')		
		Spikelet no.	Heading date	No. of plants	Spikelet no.	Heading date	No. of plants
'Noa'		26.6±0.68	127.4±0.51	5			
'Mara'		21.0±0.83	113.8±1.39	5			
F_1 ('Mara' × 'Noa')					22.4±0.40	106.6±0.68	5
Monosomics for							
	1A	21.5±0.50	110.8±1.31	4	21.8±0.20	103.8±0.20	5
	1B	22.0±0.55	110.0±0.32	5	23.5±0.29	103.0±0.91	4
	1D	21.4±0.51	115.0±1.10	5	21.8±0.25	106.3±0.25	4
	2A	22.3±0.25	111.8±1.18	4	22.6±0.40	103.4±0.24	5
	2B	22.0±0.32	113.6±0.98	5	21.8±0.20	104.4±0.24	5
	2D	18.8±0.88	115.8±0.85	5	26.0±0.00	130.0±1.00	2
	3A	22.4±0.51	113.4±1.60	5	22.4±0.40	105.4±0.68	5
	3B	23.5±0.29	111.5±0.65	4	23.6±0.24	104.8±0.37	5
	3D	21.8±0.49	111.4±0.68	5	19.8±0.49	105.2±0.49	5
	4A	20.0±0.58	109.5±0.87	4	21.4±0.24	107.6±0.60	5
	4B	23.2±0.20	112.2±0.86	5	22.8±0.20	105.8±0.20	5
	4D	21.0±0.45	113.4±0.40	5	20.4±0.51	107.2±0.97	5
	5A	20.0±0.45	115.6±0.93	5	22.2±0.37	107.2±0.58	5
	5B	22.8±0.25	115.0±0.71	4	22.6±0.24	108.0±0.32	5
	5D	23.4±0.60	114.8±1.56	5	23.0±0.45	106.8±0.37	5
	6A	20.8±0.48	112.8±0.63	4	22.8±0.25	104.8±0.25	4
	6B	22.3±0.63	124.0±1.87	4	22.3±0.25	110.0±0.71	4
	6D	20.0±1.68	115.8±0.85	4	23.0±0.32	105.6±0.51	5
	7A	20.3±0.63	115.3±1.03	4	19.8±0.37	105.6±0.60	5
	7D	21.0±0.45	111.4±0.93	5	20.7±0.33	108.3±0.33	4

soil at 25 seeds per 1 m, in rows 25 cm apart. Fertilizer, composed of 20% N, P and K, was added several times before irrigation at an overall rate of 70 g m^{-2}. Only monosomic plants, selected cytologically at meiosis, were analysed.

(3) F_2 monosomic analysis, 1985: 20 different progenies comprising 17 F_2 populations derived from F_1 hybrids monosomic for different chromosomes, a euploid F_2 population and the two euploid parental lines were analysed. In all, 25 seeds of each progeny were planted in a single row, 1 m long, in six randomized blocks. The rows were spaced 25 cm apart. The sowing date and the growth conditions were the same as described for the F_1 analysis of 1985.

Table 3. Means ± SE and variances of heading date (days from seedling emergence) and spikelet number in the main spike of the lines 'Noa', 'Mara' and of the F_2 progenies derived from crosses of 'Noa' with the monosomic series of 'Mara'. The correlation between spikelet number and heading date is given for each line

Line	Spikelet no.		Heading date		Correlation coefficient between spikelet no. and heading date*
	Mean ± SE	Variance	Mean ± SE	Variance	
'Noa'	26.1±0.12	2.06	126.4±0.1	1.4	0.08 NS
'Mara'	21.6±0.13	2.05	114.2±0.2	4.5	0.05 NS
Euploid F_2 progeny ('Mara' × 'Noa')	22.7±0.27	4.24	107.2±1.3	97.2	0.52
F_2 progenies derived from F_1 hybrids ('Mara' × 'Noa') monosomics for:					
1A	22.0±0.18	4.64	108.0±0.7	61.7	0.50
1B	23.7±0.21	6.05	108.7±1.0	124.9	0.69
2A	22.4±0.24	7.76	110.1±0.9	120.5	0.59
2B	23.5±0.24	7.64	109.7±1.0	133.3	0.69
2D	26.7±0.16	3.20	129.8±0.3	10.9	0.12 NS
3A	22.9±0.19	5.00	108.9±1.1	156.9	0.69
3B	23.3±0.20	5.71	106.6±1.0	136.2	0.65
4A	22.7±0.30	11.40	111.6±1.2	183.9	0.64
4B	23.5±0.19	4.59	108.2±0.9	106.0	0.74
5A	22.0±0.22	6.35	107.7±0.9	115.9	0.68
5B	22.9±0.21	5.61	108.4±0.8	89.1	0.67
5D	22.6±0.26	9.27	109.3±0.9	125.5	0.79
6A	22.1±0.22	6.41	107.0±1.0	130.5	0.67
6B	23.1±0.28	9.63	112.6±0.9	108.8	0.55
6D	23.4±0.22	6.70	110.1±0.9	118.5	0.65
7A	20.8±0.27	9.87	110.1±1.0	129.5	0.46
7D	22.6±0.25	8.13	109.6±1.0	124.8	0.62

* All significant ($P \leq 0.0001$) except values denoted by NS

Results

F_1 monosomic analysis, 1984

'Mara' and 'Noa' headed at about the same time, significantly later than their F_1 hybrid and most of the monosomic F_1 hybrids (Table 1). Only the hybrid which lacked 'Mara's' 2D chromosome and carried 'Noa's' 2D in a hemizygous state exhibited the parental late heading date. All other monosomic hybrids showed only a slight deviation in heading date compared to the disomic F_1 hybrid – either delay (1A, 1B, 6B) or earliness (5A, 7D).

'Noa' surpassed 'Mara' by 1.5 spikelets per spike, while both had significantly more spikelets than the F_1. Only the F_1 hybrid monosomic for 2D had as many spikelets as 'Noa'. The F_1 monosomic for 5D had a moderately, yet significantly higher number of spikelets than the disomic F_1. F_1 monosomics for 5A or for 7A had significantly fewer spikelets.

Monosomic analysis of 'Mara' and of F_1 hybrids ('Mara' × 'Noa'), 1985

The differences in spikelet number and heading date between 'Noa' and 'Mara' were greater this year than in the previous one (Table 2). The F_1 hybrid was similar to 'Mara' in its spikelet number but headed significantly earlier. The monosomic 6B line of 'Mara' headed significantly later than 'Mara'. The monosomic 2D line of 'Mara' was the only line with a significantly reduced number of spikelets.

The F_1 monosomic for 2D was the only hybrid that headed significantly later and had more spikelets than the euploid F_1. The heading date of the F_1 hybrid monosomic for 6B was delayed by only 3.4 days

F_2 monosomic analysis, 1985

In this experiment, the mean values of spikelet number and heading date of the parental lines and of the F_2 progenies were quite similar to those of the parental lines and the corresponding F_1 hybrids in the 1985 analysis (Table 3). Only the F_2 progeny derived from the monosomic 2D hybrids showed a considerable and significant delay in heading date with small variations among plants. In this progeny, the mean spikelet number was similar to that of 'Noa' and much higher than those of 'Mara' and the other F_2 progenies. The F_2 progeny lacking the 6B chromosome of 'Mara' headed

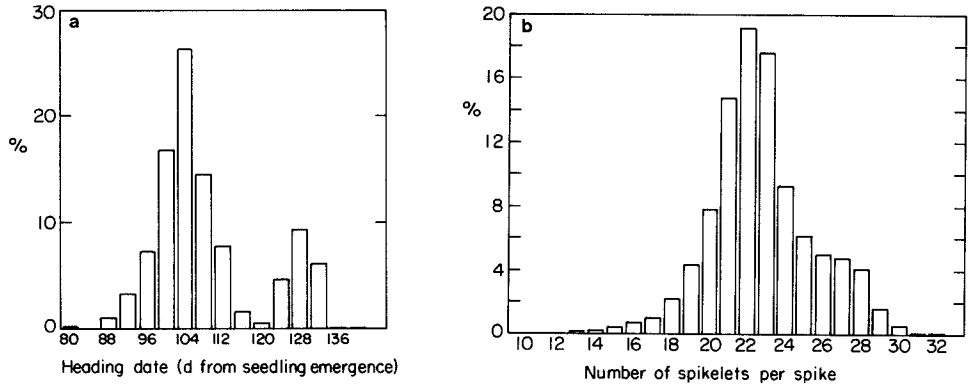

Fig. 1. Frequency distribution of heading date (**a**) and of spikelet number (**b**) in the pooled F_2 progeny derived from monosomic F_1 ('Mara' monosomic series × 'Noa') plants. The F_2 progeny originating from 'Mara' monosomic for 2D was not included

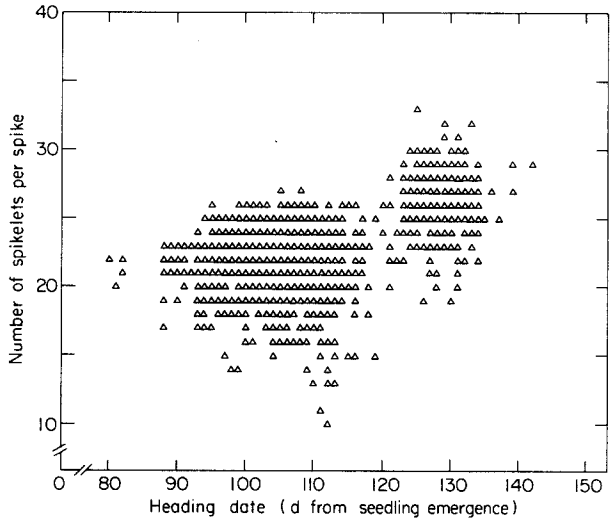

Fig. 2. Scatter diagram showing the relationship between heading date and spikelet number in the pooled F_2 progeny derived from monosomic F_1 ('Mara' monosomic series × 'Noa') plants. The F_2 progeny originating from 'Mara' monosomic for 2D was not included

slightly later than the euploid F_2 progeny. In all F_2 progenies, the correlation between spikelet number and heading date was significant, ranging from 0.46 to 0.79, with the exception of the 2D progeny that showed a non-significant and low correlation coefficient.

All F_2 progenies derived from monosomic plants, excluding that derived from F_1 monosomic 2D, were pooled to give a population with 79% early heading plants (85–119 days from sowing) and 21% late heading plants (120–140 days; Fig. 1a). The distribution of spikelet number in this pooled population was quite a normal one, with about half the plants having less than 23 spikelets per spike (Fig. 1b). Consequently, the pooled F_2 population could be divided into two distinct groups (Fig. 2): 'early-heading' with 'few' spikelets, and 'late-heading' with 'many' spikelets. There was a considerable overlap in the number of spikelets per spike between the two heading-date groups. The distribution of spikelet number within both groups was negatively skewed in a similar manner.

Discussion

In the 1985 experiment, 'Noa' exhibited its usual late heading date, heading significantly later than 'Mara'. The similar heading date of 'Mara' and 'Noa' in 1984 could be ascribed to the late December planting, which presumably induced in 'Noa' a faster development than usual. Nevertheless, even in 1984, and more so in 1985, the F_1 hybrid between 'Mara' and 'Noa' headed earlier than 'Mara'. These findings indicate that 'Noa' and 'Mara' possess different alleles for heading date at different loci. In all cases, 'Noa' surpassed 'Mara' in spikelet number, with the least difference between them in the 1984 experiment. Spikelet number of the F_1 hybrid was either similar or lower than that of 'Mara'. These data confirm the reports of Millet (1983, 1986b) that 'Noa' carries recessive alleles both for late heading date and and for a large number of spikelets per spike.

The monosomic analyses revealed several chromosomes carrying alleles for heading date and spikelet number which distinguish 'Noa' from 'Mara'. In 'Noa', major effects of delaying heading date and of increasing spikelet number can be attributed to genes located on chromosome 2D, as revealed in the F_1 hybrid (1984 and 1985 experiments) and in the F_2 progenies. Since the genes for these traits could be detected in the F_1 hybrids lacking 'Mara's' 2D chromosome, they should be considered recessive. The effect of 'Noa's' 2D chromosome on the build-up of spikelet number and on the determination of heading

date was discussed by Millet (1986 b), who detected on this chromosome a recessive allele acting on the prolongation of the post-differentiation phase. On the other hand, the allele coding for a large initial number of spikelets, being a dominant one, could not be detected in the F_1 hybrid monosomic for 2D. In the current F_2 analysis, several chromosomes of 'Noa' increased the spikelet number slightly but significantly. One of these may have carried the allele conferring the large initial number of spikelets which contributed to the final number (Millet 1986 a).

Considering the late heading date both of 'Mara' monosomic 2D and of the monosomic F_1 hybrid derived from it (Table 2), the mean late heading date of the F_2 progeny lacking 'Mara's' 2D chromosome could have been attributed to the presence of only one dose of 'Noa's' 2D chromosome, which presumably existed in about 75% of this progeny (Sears 1953). However, chromosome counts at meiosis, performed on a sample of this progeny selected for various heading dates, showed no correlation between this trait and the dosage of the 2D chromosome. Thus the late mean heading date in this progeny was due to the expression of an allele located on 'Noa's' 2D rather than to the hemizygous state. This finding also confirms that the allele affecting heading date is different from the *ppd1* of 'Mara', which was found to be dosage-dependent (Millet 1986 b; Scarth and Law 1984). The higher variation in heading date of this progeny, compared to the parental variation, could be attributed to segregation of other genes with minor effects located on other chromosomes.

Other chromosomes showed minor effects on heading date and spikelet number. Deletion of 'Mara's' 6B chromosome from the F_1 hybrid and from the F_2 progeny, or from 'Mara' itself, delayed the heading date – an indication that 'Mara' carries on this chromosome a dominant allele for early heading date. Similarly, using reciprocal monosomic hybrids, Hoogendoorn (1984) found that the cultivars 'Bersee' and 'Spica' carry on their 6B chromosome different alleles for earliness. An indication of a recessive allele for spikelet number on 'Noa's' 5D chromosome was evident in the F_1 hybrid but not in the F_2 progeny lacking 'Mara's' 5D chromosome. On the other hand, a recessive allele that acts by slightly decreasing spikelet number was detected on chromosome 7A of 'Noa'.

A major effect of only one chromosome on heading date was also evident in the segregating F_2 population. Excluding the progeny derived from 'Mara' monosomic 2D, the pooled F_2 progeny segregated in a ratio of 3 'early heading' : 1 'late heading'. On the other hand, the spikelet number of this progeny followed quite a normal distribution. The variances in spikelet number, both in the 'late heading' progeny – apparently possessing 'Noa's' 2D chromosomes – and in the 'early heading' progeny – possessing 'Mara's' 2D or heterozygous for it – were significantly greater than those of any parent, indicating that additional genes for spikelet number segregated in both progenies. The negatively skewed distribution of spikelet number in any of the 'early heading' and 'late heading' progenies indicates that these additional genes are dominant. These data suggest that the genes with minor effects on spikelet number are located on chromosomes other than 2D, rather than recombining with the major gene on 2D – otherwise the segregation of spikelet number within each heading group would have been differently skewed. One of these minor genes might affect the spikelet number through an increase in the initial spikelet primordia, as previously suggested.

A recessive major allele for late heading date associated with a large number of spikelets per spike was found on chromosome 2D of 'Noa'. Additional dominant alleles that also contribute to the large number of spikelets per spike are located on chromosomes other than 2D of 'Noa'. In the F_1 analysis of heading date components and build-up of spikelet number (Millet 1986 b), the differences in the final spikelet number were too small to be ascribed to the differences in the determinants of spikelet number, namely, to the initial spikelet number, and to the rate and duration of spikelet production. It could be assumed that the recessive allele for late heading date is associated with a long spikelet phase and that the dominant allele for a large number of spikelets is expressed by a large initial spikelet number.

A better understanding of the action of each allele and the relationships between them would be possible when a pair of 'Noa's' 2D chromosomes replace the homologous pair of 'Mara' on the latter's background. Such an intervarietal substitution line is now in preparation at our laboratory.

Acknowledgements. The author is very grateful to Mrs. Ilana Strauss for the cytological analysis and to Mr. Yigal Avivi for his assistance in the preparation of the manuscript.

References

Halse NJ, Weir RN (1970) Effect of vernalization, photoperiod and temperature on the phenological development and spikelet number of Australian wheat. Aust J Agric Res 21:383–393

Hoogendoorn J (1984) A reciprocal F_1 monosomic analysis of the genetic control of time of ear emergence, number of leaves and number of spikelets in wheat (*Triticum aestivum* L.). Euphytica 34:545–558

Millet E (1983) Breeding for larger number of spikelets per spike in wheat. In: Proc 6th Int Wheat Genet Symp, Kyoto, Japan, pp 623–628

Millet E (1986a) Developmental differences between wheat lines with regular and multispikelet spike. Z Pflanzenzücht 96:265–270

Millet E (1986b) Genetic control of heading date and spikelet number in common wheat (*T. aestivum* L.) line 'Noa'. Theor Appl Genet 72:105–107

Pinthus MJ (1963) Inheritance of heading date in some spring wheat varieties. Crop Sci 3:301–304

Rahman MS, Wilson JH (1977) Determination of spikelet number in wheat. I. Effect of varying photoperiod on ear development. Aust J Agric Res 28:565–574

Rawson HM (1971) An upper limit for spikelet number per ear in wheat as controlled by photoperiod. Aust J Agric Res 22:537–546

Sears ER (1953) Nullisomic analysis in common wheat. Am Nat 87:245–252

Scarth R, Law CN (1984) The control of day-length response in wheat by the group 2 chromosomes. Z Pflanzenzücht 92:140–150