Theor Appl Genet (1986) 72, 105–107

Genetic control of heading date and spikelet number in common wheat (*T. aestivum* L.) line 'Noa'

E. Millet

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

Received July 30, 1985; Accepted October 10, 1985
Communicated by J. MacKey

Summary. The phenology and build-up of spikelet number under 10 h day-length were studied in five wheat lines: the multispikelet line 'Noa', the regular line 'Mara', the F_1 hybrid between them and monosomics 2D of 'Mara' and of this hybrid (lacking the 2D chromosome of 'Mara'). 'Noa' had a longer spike development phase, a higher initial number of spikelet primordia and a slower rate of spikelet production than 'Mara'. The F_1 hybrid was similar to 'Noa' in its high initial number of spikelets and to 'Mara' in its high rate of spikelet production. This hybrid had a shorter spikelet phase than both parents. Deletion of one dose of the 'Mara' 2D chromosome from either 'Mara' or the F_1 hybrid caused a reduction in the rate of spikelet production and an increase in the duration of the spikelet phase. These effects were due to the reduced dosage of the 2D chromosome. However, in the F_1 hybrid this deletion also caused an increase in the spike development phase – an indication that 'Noa' carries on its 2D chromosome a recessive gene for late heading date which acts on the spike development phase. This gene of 'Noa' is independent of the day-length sensitive gene *ppd*, and is different from 'Noa's dominant gene for large initial number of spikelets.

Key words: Wheat – *T. aestivum* – Heading date – Spikelet number – Phenology – Day-length insensitivity

Introduction

Two photoperiod responsive genes have been identified on group 2 chromosomes of common wheat (*Triticum aestivum* L.): *Ppd1* on 2D and *Ppd2* on 2B (Welsh et al. 1973; Scarth and Law 1983). An additional photoperiod gene (*Ppd3*) was suggested by Scarth and Law (1983) to be located on the homoeologous chromosome 2A. Alleles conferring photoperiod insensitivity (*Ppd*) have been defined as those inducing early heading date under short day-length (Scarth and Law 1984).

Various lines were found to carry different alleles for day-length insensitivity (Scarth and Law 1984; Welsh et al. 1973). Other genes that affect heading date, in addition to the day-length responsive ones, are also considered to be located on crhomosome 2B and on other chromosomes of this group (Scarth and Law 1983, 1984).

Detailed information on the effect of *Ppd* genes on the phenology and build-up of spikelet number is limited. Worland et al. (1983) reported that autumn sown lines carrying the insensitive allele *Ppd1* developed more rapidly and headed earlier than lines carrying *ppd1*. However, the latter attained a higher number of spikelets. Scarth et al. (1985) showed that plants carrying either *Ppd1* or *Ppd2* had a shorter spikelet phase and a faster apex development than those carrying the recessive alleles.

We have recently reported on the developmental features of 'Noa' – a late-heading multispikelet line (Millet 1983). Aiming to allocate to chromosomes the genes controlling these traits, we utilized a monosomic series of 'Mara' – a regular line known to carry the day-length insensitive gene (*Ppd1*) on its 2D chromosome (Worland et al. 1983). This study has already revealed that F_1 ('Mara' × 'Noa') monosomic 2D plants head considerably later than most other monosomic lines and have a large number of spikelets per spike (unpublished data). These findings could be ascribed to the presence of recessive alleles derived from 'Noa' or to the hemizygous 2D chromosome since dosage effect of group 2 chromosomes on day-length sensitivity has been reported (Scarth and Law 1984).

Considering that both the number of spikelets per spike and heading date are complex traits which largely interact with each other, we used monosomic plants in order to assess the role of 2D chromosome of 'Mara' and 'Noa' on the phenology and build-up of spikelet number.

Materials and methods

The following hexaploid wheat lines (*T. aestivum* L.) were used: 'Noa' (an Israeli late-heading multispikelet line); 'Mara' (a regular line); 'Mara' monosomic 2D line, kindly provided by B. Giorgi, ENEA, Italy; the F_1 hybrid ('Mara'×'Noa') and the F_1 ('Mara'×'Noa') monosomic 2D. Plants were grown in a greenhouse under controlled conditions of 10 h day length of natural daylight and 18/10 °C day/night temperature. Monosomic plants were selected by cytological examination of root-tip cells.

Several plants from each of the above lines were sampled and dissected to determine the stages of double ridges (DR) and the initiation of the terminal spikelet primordium (TS). In the monosomic F_1 hybrid, only one plant was examined for the determination of the DR stage because of a lack of these plants. However, those plants sampled just four days earlier had an elongated vegetative apex, whereas four days later – swollen ridges were apparent.

The durations of the developmental phases were calculated as follows: vegetative phase – from seedling emergence to DR; spikelet phase – from DR to TS and spike development from TS to heading. The rate of spikelet production was obtained by dividing the number of spikelets added after the DR stage by the duration of the spikelet phase.

Results and discussion

Data on the phenology and build-up of spikelet number of the five tested lines are summarized in Table 1. In a previous study 'Mara' was found to carry the day-length insensitive allele *Ppd1* on its 2D chromosome (Worland et al. 1983). Monosomic 2D 'Mara', carrying the *Ppd1* allele in only one dose, headed 13 days later than the euploid 'Mara'. In view of the dosage effect of group 2 chromosomes on heading date (Scarth and Law 1984), this delay was expected. Moreover, since this delay is completely accountable for by the prolongation of the spikelet phase, it may be assumed that this gene acts specifically on this phase. Indeed shortening the duration of the spikelet phase was the main effect of substituting *ppd1* or *ppd2* by their respective dominant alleles (Scarth et al. 1985). Similarly, prolongation of this phase was observed in the monosomic F_1 hybrid lacking the 2D chromosome of 'Mara'. However, the F_1 hybrid had also a short spike development phase – similar to its parent 'Mara' which carries the dominant allele for this trait. When the 2D chromosome of 'Mara' was deleted from this hybrid, a recessive allele of 'Noa' acting on the spike development phase, was expressed, explaining the long duration of this phase in this hybrid. Thus, the data indicate that 'Noa' possesses on its 2D chromosome a recessive allele, other than the *ppd1* gene, for a prolonged spike development phase.

In no case did the absence of the 2D chromosome affect the duration of the vegetative phase, indicating that this phase is under a separate genetic control. This is supported by the results obtained by Scarth et al. (1985) who found a similar vegetative phase for *Ppd1* and *ppd1* or for *Ppd2* and *ppd2* plants.

Under the short days which prevailed in this experiment, 'Noa', like 'Mara', had a short spikelet phase, presumably also indicating the presence of a *Ppd* allele in 'Noa'. In a previous study carried out under a similar photoperiod (Millet 1986), 'Noa' was reported to have a longer spikelet phase and a shorter spike development phase than reported here – probably due to different temperatures or day-light intensities prevailing in the two experiments. The fact that the F_1 hybrid between 'Mara' and 'Noa' had a shorter spikelet phase than 'Mara' may indicate that in 'Noa' this allele for day-length insensitivity is located on a chromosome other than 2D.

'Noa' surpassed 'Mara' significantly in the initial number of spikelet primordia, counted at the DR stage (Fig. 1). The superiority of 'Noa' over other lines regarding this trait has been previously recorded (Millet 1986). The high initial number of spikelets in the F_1 hybrid revealed that this trait is a dominant one. No relationships existed between this characteristic and the duration of the vegetative phase. This is in contrast to the suggestion of Halse and Weir (1970) that the initial number of spikelets at the DR stage is affected by the duration of the vegetative phase. Only a slight difference in the final spikelet number between 'Noa' and 'Mara' was observed in this experiment. However, when

Table 1. Phenology (in days) and build-up of spikelet number in the multispikelet line 'Noa', the regular line 'Mara', the F_1 hybrid between them and in monosomic 2D of 'Mara' and of this hybrid

Line	Duration of developmental phases (d ± SE)			Initial spikelet no.[b]	Final spikelet no.	Rate of spikelet production (d^{-1})
	Vegetative	Spikelet	Spike development			
'Noa'	39.3±0.67	16.0±2.54	73.4±2.46	15.0±1.73	27.4±0.32	0.78
'Mara'	42.0±0.00	20.0±1.83	57.0±3.00	5.5±0.50	25.9±0.31	1.02
Mono 2D 'Mara'	41.0±1.00	34.5±1.58	56.5±0.71	7.5±0.50	27.0±0.58	0.57
F_1 ('Noa'×'Mara')	38.0±0.41	12.7±0.82	52.1±2.50	13.8±0.48	26.2±0.29	0.98
Mono 2D F_1 ('Nora'×'Mara')	39[a]	24[a]	78.0±8.0	17[a]	29.0±0.58	0.50

[a] Based on one plant (see "Materials and methods")
[b] Spikelet primordia at 'double ridges'

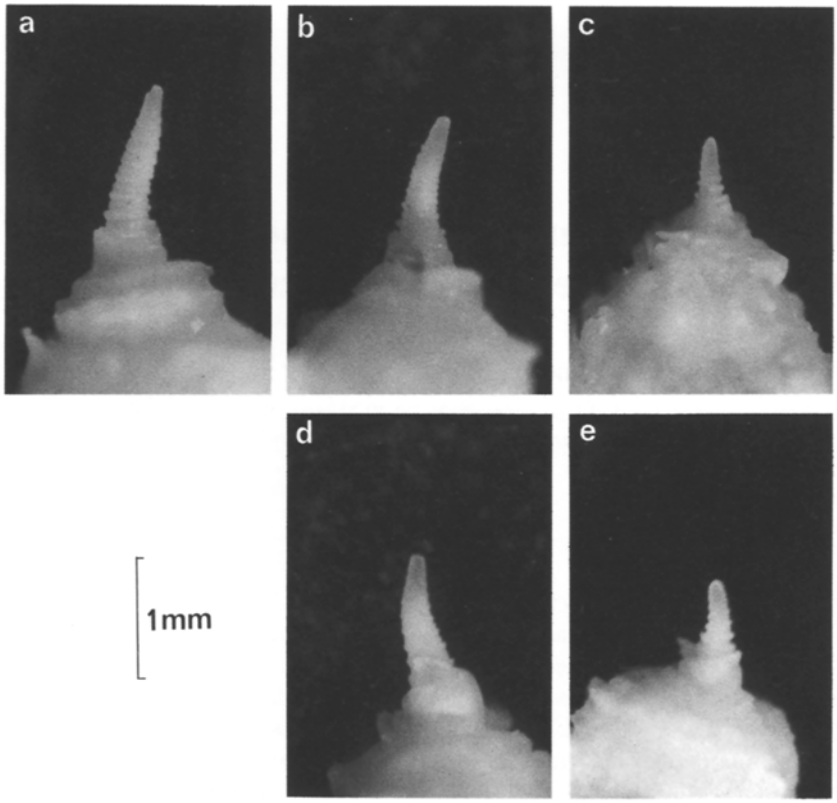

Fig. 1a–e. Apices of the different lines at the 'double ridges' stage. Upper row – euploid lines; lower row – monosomic lines. **a** 'Noa'; **b** F_1 ('Mara × Noa'); **c** 'Mara'; **d** Monosomic 2D F_1 ('Mara' × 'Noa'); **e** Monosomic 2D Mara

the two lines were autumn sown and grown outdoors larger differences were recorded (26.2 and 21.6 spikelets in 'Noa' and 'Mara', respectively; unpublished data). It seems that the conditions prevailing in the current experiment induced relatively high spikelet number in 'Mara'. Yet, significant differences between 'Noa' and 'Mara' in certain developmental features were apparent in this experiment.

The number of spikelets added after the DR stage either to 'Mara' or to the F_1 hybrid was independent of the dosage of the 2D chromosome: about 20 and 12 spikelets for 'Mara' and the F_1, respectively. Consequently, the increase in the duration of the spikelet phase due to the 2D hemizygous situation caused a conspicuous decrease in the rate of production of these spikelets.

'Noa's large number of spikelets per spike, which is largely due to its high initial number of spikelets (Millet 1986) was found to be under a separate control from the duration of spike development phase which contributed to its late heading-date. In this study it was impossible to locate the gene for the initial spikelet number due to its dominance. Irrespective of whether both genes are located on the same or on different chromosomes, it may be possible to combine the desirable alleles in an attempt to obtain early lines with many spikelets.

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 vernaligation, photoperiod and temperature on the phenological development and spikelet number of Australian wheat. Aust J Agric Res 21:383–393

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

Millet E (1986) Developmental differences between wheat lines with regular and multispikelet spikes. Z Pflanzenzücht (in press)

Scarth R, Kirby EJM, Law CN (1985) Effects of the photoperiod genes *Ppd*1 and *Ppd*2 on growth and development of the shoot apex in wheat. Ann Bot 55:351–359

Scarth R, Law CN (1983) The location of photoperiod gene *Ppd2,* and an additional genetic factor for ear emergence time on chromosome 2B of wheat. Heredity 51:607–619

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

Welsh JR, Keim DL, Pirasteh B, Richards RD (1973) Genetic control of photoperiod response in wheat. In: Sears ER, Sears LMS (eds) Proc 4th Int Wheat Genet Symp. University of Columbia, Missouri, pp 879–884

Worland AJ, Law CN, Parker BB (1983) Alternative semidwarfing genes. In: Annu Rep Plant Breed Inst. Cambridge, pp 59–61