Factors in the Reduction in Grain Number in Winter Wheat by Early-Sowing in Yamaguchi

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Abstract: Grain number per spike of wheat is lower in early sowing than in the conventional standard cultivation in Yamaguchi, Prefecture, Japan. Components of the grain number per spike in five cultivars were analyzed with respect to temperature during the spike development period throughout three growing seasons 2001/2002, 2002/2003 and 2003/2004 to find the cause of the problem of early sowing cultivation. The plants sown in early-October and late-November were called the early sown group and the standard group, respectively, in the following. Three of the five cultivars, Hokushin, Akitakko and Nanbukomugi, showed a strong winter habit, which requires very cold temperatures for spike differentiation. The other two cultivars, Iwainodaichi and Airakomugi, had a moderate winter habit. Grain number per spike and grain yield were decreased by early-sowing (compare with the standard group) in almost all cultivars throughout the three growing seasons. The three cultivars which had a strong winter habit had fewer spikelets per spike in the early-sown group than in the standard group. The other two cultivars which had a moderate winter habit had fewer grains per spikelet in the early-sown group. The higher the temperature during the spikelet formation phase, which is from flag leaf initiation to terminal spikelet initiation, the higher the number of spikelets per spike in the standard group. The spikelet number per spike in the early-sown group increased with the increase in productive tillers under fertile conditions. Such conditions also increased the grain number per spike.

Key words: Early sowing cultivation, Grain number per spike, Grain number per spikelet, Multiple regression, Spike development period, Spikelet number per spike, Temperature, Winter wheat cultivar.

We usually use a spring-type cultivar for wheat cultivation in Yamaguchi Prefecture, Japan. It is sown in mid or late November and harvested in early July. Sowing is sometimes delayed because of wet field conditions in November. When we have heavy rains in November when the temperature turns low, the wet fields hardly ever dried out. Delayed sowing leads to delayed harvesting in the rainy season, resulting in a poor production. Early sowing is one of the measures taken to avoid such problems. Our previous report showed that early sowing of winter-type cultivars did not advance to the stem elongation stage because of autumn warm, and winter cold did not kill spikes in their main stems, nor were their grain yields reduced considerably (Zhang et al., 2006). While the winter-type cultivars showed higher grain yields than the springs, their grain yield of winter cultivars was lower in early sowing cultivation, the early October, than in the conventional standard, the late November. The lower yield in early sowing cultivation was due to fewer spike numbers and fewer grain numbers per spike, with the latter being mainly due to fewer grain numbers per spikelet (Zhang et al., 2006).

Spikelet number per spike is considered to be determined by the number of primordia differentiated during the period from flag leaf initiation to terminal spikelet initiation. Grain number per spikelet is determined by the number of florets that differentiated and grown from terminal spikelet initiation to anthesis (Gonzalez et al., 2005). Grain number per spike has been thought to be determined by the spike growth during this latter stage during which the stem elongates (Fischer, 1985; Slafer et al., 2001; Gonzalez et al., 2005).

Spike development is accelerated as temperature increases during the period from flag leaf initiation to anthesis when the grain number per spike is determined (Rahman and Wilson, 1978; Slafer and Rawson, 1994). It is also accelerated as the photoperiod increases (Evans and Wardlaw, 1976). Coldness also influences spike development. Grain number per spike varies with the cultivar depending on the responses to temperature and daylength of each cultivar (Takahashi and Nakaseko, 1992; Slafer and Rawson, 1994; Fukushima et al., 2001). Our previous study (Zhang et al., 2006) also showed that the spike number and spikelet number per spike are changed by early sowing. The temperature in Yamaguchi falls during the spike development stage from autumn to winter when the grain number per
spike is determined, then rises from winter to spring. Our previous study (Zhang et al., 2006) showed that winter-type cultivars had an advantage over spring-type ones because they could avoid cold damage during their spike development phase. In order to establish the method of early sowing cultivation, we have to need know how the early sowing of these winter-type cultivars affects their developmental stage. Changes in the development stage must affect the spikelet number per spike and the grain number per spikelet. In this study we investigated the effect of changes in temperature induced by early sowing on the components of grain number per spike, (spikelet number per spike and the grain number per spikelet) of winter-type cultivars.

Materials and methods

1. Cultivation of materials

Field experiments were conducted at the Experimental Farm of Faculty of the Agriculture, Yamaguchi University, in three growing seasons, 2001/2002, 2002/2003, and 2003/2004. Winter wheat cultivars were sown in early-October and late-November, and they were called the early-sown group and the standard group, respectively. Five cultivars Hokushin, Akitakko, Nanbukomugi, Iwainodaichi and Airakomugi were grown in 2001/2002 and 2002/2003, and Akitakko, Iwainodaichi and Airakomugi in 2003/2004. Three of the five cultivars, Hokushin, Akitakko and Nanbukomugi, had a strong winter habit, which requires cold temperatures to differentiate spikes. The other two cultivars, Iwainodaichi and Airakomugi, had a moderate winter habit. In the early-sown and standard groups, seeds were sown on October 4 and November 21 in 2001/2002, on October 1 and November 19 in 2002/2003, and on October 7 and November 18 in 2003/2004, respectively. Four hundred seeds per square meter were sown in with 20-cm row spacing, and the seedlings with two or three leaves were thinned to 200 plants per square meter. Fertilizer was applied only as basal dressing in all growing seasons at a rate of 16 gm$^{-2}$ of N, 10 gm$^{-2}$ of P$_2$O$_5$ and 8 gm$^{-2}$ of K$_2$O.

2. Determination of dates of double ridge stage and terminal spikelet initiation

The stages of the flag leaf initiation, the double ridge stage and the terminal spikelet initiation were determined by observation of the shoot apexes of three main stems under a microscope at 1- to 7-day intervals (Fig. 1). Flag leaf initiation was determined by the confirmation of the flag leaf primordium. The double ridge stage was defined as the period when both of the primordia bract and spikelet primordia were visible in the shoot apex (Porter et al., 1987). The terminal spikelet stage is defined as the period when the terminal spikelet differentiated in the shoot apex.

3. Determination of grain number per spike, spikelet number per spike and grain number per spikelet

Grain yield was measured in three 0.6-m$^2$ plots that were arranged in a randomized block design. All plants in each plot were cut off at ground level, and their spikes were counted. Thirty of the spikes were randomly selected to determine the spikelet number in each season. All the plants were dried for 48 hours at 80°C and weighed to determine the biomass yield. All spikes were hand-threshed to determine the grain yield and grain weight. The number of grains per spike was also calculated from the grain yield, spike number and grain weight.

The temperature data were from the Yamaguchi weather bureau.
Table 1. Grain yield and yield components in the early-sown group and the standard group in three growing seasons.

| Growing season | Cultivar       | Grain yield (g/m²) | Spike number (m⁻²) | Grains per spike | Grain weight (mg) |
|----------------|---------------|--------------------|--------------------|------------------|-------------------|
|                | Early-sown    | Standard group     | RES (%)            | Early-sown group | Standard group    | RES (%)          |
|                | Standard group|                    |                    |                  |                   |                  |
| 2001/2002      | Hokushin      | 105                | 127                | -17.4**          | 333               | 277              | 29.2**          | 13.0             | 17.3             | -24.8*           | 24.3             | 26.0             | -6.7**           |
|                | Akitakko      | 163                | 151                | 8.4**            | 297               | 288              | 3.3**           | 18.4             | 21.0             | -12.3**          | 29.9             | 25.1             | 19.1*            |
|                | Nanbukomugi   | 114                | 156                | -26.9**          | 232               | 248              | 1.6**           | 14.7             | 21.3             | -31.3**          | 31.0             | 28.7             | 7.9**            |
|                | Iwainodaichi  | 151                | 256                | -40.9*           | 272               | 371              | -26.7**         | 19.1             | 23.1             | -17.3**          | 28.2             | 29.5             | -4.4**           |
|                | Airakomugi    | 176                | 202                | -12.8**          | 326               | 359              | -9.3**          | 17.4             | 21.7             | -19.9            | 30.9             | 25.6             | 20.6**           |
| 2002/2003      | Hokushin      | 297                | 317                | -6.3**           | 499               | 489              | 2.0**           | 21.3             | 22.5             | -5.5**           | 27.6             | 28.8             | -4.2**           |
|                | Akitakko      | 362                | 235                | 53.9*            | 482               | 481              | 0.2**           | 25.6             | 27.4             | -6.6**           | 29.6             | 17.9             | 65.6**           |
|                | Nanbukomugi   | 303                | 437                | -30.6**          | 390               | 479              | -18.7**         | 22.5             | 26.9             | -16.4**          | 34.3             | 33.9             | 1.2**            |
|                | Iwainodaichi  | 328                | 560                | -39.6*           | 584               | 702              | -16.7           | 20.8             | 24.4             | -14.9**          | 27.9             | 32.9             | -15.1**          |
|                | Airakomugi    | 321                | 444                | -27.7**          | 385               | 663              | -42.0**         | 25.2             | 23.6             | 6.0**            | 33.1             | 28.9             | 14.5**           |
| 2003/2004      | Akitakko      | 424                | 242                | 75.3**           | 592               | 417              | 42.1**          | 26.6             | 20.9             | 27.4**           | 26.8             | 26.8             | 0.0**            |
|                | Iwainodaichi  | 285                | 425                | -33.0*           | 483               | 596              | -18.9**         | 18.6             | 22.2             | -16.5**          | 31.7             | 32.6             | -2.7**           |
|                | Airakomugi    | 275                | 424                | -35.2**          | 468               | 621              | -24.7**         | 20.2             | 20.6             | -1.9**           | 28.6             | 32.2             | -11.2**          |

*, Significant at the 10% level. *, Significant at the 5% level. **, Significant at the 1% level. NS, Not significant. RES, Rate of increase by early sowing.

Results

1. Grain yield and yield components

Table 1 shows grain yield and yield components in the early-sown group and the standard group in three growing seasons. Grain yield was decreased by early sowing in four of the five cultivars throughout all the three growing seasons. Only in Akitakko was the grain yield increased by early sowing. All cultivars had the lowest grain yield in the 2001/2002 season.

The spike number decreased by early sowing in Iwainodaichi and Airakomugi which had a moderate winter habit, but it was not influenced by early sowing in Hokushin, Akitakko and Nanbukomugi, which had a strong winter habit. Grain number per spike was reduced by early sowing in all cultivars in all three growing seasons except for Airakomugi in 2002/2003 and Akitakko in 2003/2004. Grain weight showed no obvious correlation with sowing period regardless of cultivar and growing season.

Table 2 shows spikelet number per spike and grain number per spike in the early-sown and standard groups throughout the three growing seasons.

Spikelet number per spike was reduced by early sowing in Hokushin, Akitakko and Nanbukomugi, which had a strong winter habit, in both 2001/2002 and 2002/2003, but was slightly increased by early sowing in Iwainodaichi, which had a moderate winter habit throughout the three growing seasons (Table 1). In Airakomugi spikelet number per spike was increased by early sowing in 2001/2002 and 2003/2004, but decreased by early sowing in 2002/2003.

Grain number per spikelet was reduced by early sowing in all cultivars in 2001/2002. In 2002/2003, however, it was increased by early sowing in Hokushin and Airakomugi, while Iwainodaichi showed a lower one in the early-sown group in 2002/2003. In 2003/2004, it was increased by early sowing in Akitakko, but was reduced in Iwainodaichi and Airakomugi.

Fig. 2 shows the frequency distribution of spikelet number per spike in the early-sown group of Airakomugi in the three growing seasons. The spikelet number per spike in the early-sown group of Airakomugi showed a normal distribution with a peak around its mean in 2001/2002 and 2003/2004. On the other hand, in 2002/2003 it had two peaks in its distribution, which were at 12-13 and at 17-18.

2. Changes in the date and temperature during spike development period by early sowing

Table 3 shows the dates of flag leaf initiation, double ridge stage, terminal spikelet initiation and anthesis in all cultivars in the early-sown and standard groups throughout three growing seasons. In the standard group, the date of flag leaf initiation was from late December to early January in Iwainodaichi and Airakomugi, which had a moderate winter habit, and in late January in Hokushin, which had a strong winter habit. On the other hand, in the early-sown group, the
date of flag leaf initiation was from late October to early November in Iwainodaichi and Airakomugi, and to mid-November for Hokushin. Dates of the double ridge stage also fell one to two months earlier for Iwainodaichi and Airakomugi than for Hokushin, and about a month earlier in the early sown group than in the standard group for all cultivars throughout three growing seasons.

Terminal spikelet initiated in late February in Iwainodaichi and Airakomugi and in early April for Hokushin in the standard group, it went from mid-December to mid-January for Iwainodaichi and Airakomugi, and to mid-March for Hokushin in the early-sown group, which was one to two months earlier than in the standard group.

Anthesis was from mid to late April in Iwainodaichi and Airakomugi and from early to mid-May in Hokushin in the standard group, and from early to late April in Iwainodaichi and Airakomugi, and to late April in Hokushin in the early-sown group.

The period from flag leaf initiation to terminal spikelet initiation was increased by early sowing in Hokushin, Akitakko and Nanbukomugi, which had a strong winter habit. The interval from terminal spikelet initiation to anthesis was increased by early sowing in Iwainodaichi and Airakomugi, which had a strong winter habit.

Fig. 3 shows the mean air temperature from October to April in the three growing seasons and an average year. The mean temperature in 2001/2002 decreased linearly from October to December similarly to that in an average year. It was lower than that in an average year in late December but was higher in mid-January. It increased linearly from February to April, and was higher than in an average year. The temperature in 2002/2003 decreased from late October to mid-

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| Growing season | Cultivar      | Spikelet number per spike | Grain number per spike |
|----------------|---------------|---------------------------|------------------------|
|                | Early-sown group | Standard group | RES (%) | Early-sown group | Standard group | RES (%) |
| 2001/2002      | Hokushin        | 18.6                    | 20.5                  | −9.3* | 0.70 | 0.84 | −17.2** |
|                | Akitakko        | 18.7                    | 19.7                  | −5.1* | 0.98 | 1.06 | −7.7* |
|                | Nanbukomugi     | 18.4                    | 19.7                  | −6.6* | 0.80 | 1.08 | −26.1* |
|                | Iwainodaichi    | 18.0                    | 17.0                  | 5.9** | 1.06 | 1.36 | −21.9* |
|                | Airakomugi      | 18.0                    | 16.7                  | 7.8*  | 0.96 | 1.30 | −25.6** |
| 2002/2003      | Hokushin        | 19.3                    | 23.1                  | −16.5* | 1.10 | 0.97 | 13.3* |
|                | Akitakko        | 20.0                    | 21.8                  | −8.3* | 1.28 | 1.26 | 1.8 NS |
|                | Nanbukomugi     | 18.7                    | 21.1                  | −11.4* | 1.20 | 1.27 | −5.6** |
|                | Iwainodaichi    | 19.7                    | 18.8                  | 4.8*  | 1.06 | 1.30 | −18.6 NS |
|                | Airakomugi      | 15.9                    | 19.2                  | −17.2** | 1.58 | 1.23 | 28.9* |
| 2003/2004      | Akitakko        | 22.2                    | 20.6                  | 7.8*  | 1.20 | 1.01 | 18.5 NS |
|                | Iwainodaichi    | 19.5                    | 17.9                  | 8.8 NS | 0.95 | 1.24 | −23.2 NS |
|                | Airakomugi      | 21.1                    | 18.1                  | 16.7* | 0.96 | 1.14 | −15.9 NS |

*, Significant at the 10% level. *, Significant at the 5% level. **, Significant at the 1% level.
NS, Not significant.
RES, Rate of increase by early sowing

Fig. 2. Frequency distribution of spikelet number per spike in the early-sown group of Airakomugi in the three growing seasons.
Table 3. Dates of flag leaf initiation, double ridge stage, terminal spikelet initiation and anthesis in all cultivars in the early-sown and standard groups throughout three growing seasons.

| Growing season | Cultivar       | Flag leaf initiation | Double ridge stage | Terminal spikelet initiation | Anthesis | FI-TS days | TS-An days |
|----------------|----------------|----------------------|--------------------|------------------------------|----------|------------|------------|
|                | Early-sown group | Standard group       | Early-sown group   | Standard group               | Early-sown group | Standard group | Early-sown group | Standard group | Early-sown group | Standard group | Early-sown group | Standard group |
| 2001/2002      | Hokushin        | 12 Nov. 27 Jan.     | 20 Feb. 15 Mar.    | 7 Mar. 1 Apr.               | 27 Apr. 4 May. | 115 64     | 51 33      |
|                | Akitakko        | 6 Nov. 21 Jan.      | 26 Jan. 4 Mar.     | 3 Mar. 19 Mar.              | 20 Apr. 28 Apr. | 117 57    | 48 40      |
|                | Nanbukomugi     | 1 Nov. 18 Jan.      | 6 Feb. 7 Mar.      | 1 Mar. 17 Mar.              | 18 Apr. 28 Apr. | 120 58    | 48 42      |
|                | Iwainodaichi    | 28 Oct. 2 Jan.      | 3 Jan. 7 Feb.      | 17 Jan. 26 Feb.             | 6 Apr. 17 Apr. | 81 55     | 79 50      |
|                | Airakomugi      | 26 Oct. 1 Jan.      | 28 Dec. 7 Feb.     | 15 Jan. 27 Feb.             | 7 Apr. 20 Apr. | 81 57     | 82 52      |
| 2002/2003      | Hokushin        | 7 Nov. 28 Jan.      | 15 Feb. 16 Mar.    | 14 Mar. 5 Apr.              | 30 Apr. 11 May. | 127 67    | 47 36      |
|                | Akitakko        | 5 Nov. 19 Jan.      | 20 Jan. 8 Mar.     | 5 Mar. 28 Mar.              | 27 Apr. 3 May. | 120 68    | 53 36      |
|                | Nanbukomugi     | 6 Nov. 20 Jan.      | 29 Jan. 11 Mar.    | 27 Feb. 26 Mar.             | 24 Apr. 1 May. | 113 65    | 56 36      |
|                | Iwainodaichi    | 2 Nov. 1 Jan.       | 15 Dec. 9 Feb.     | 11 Jan. 25 Feb.             | 23 Apr. 24 Apr. | 70 55     | 102 58     |
|                | Airakomugi      | 1 Nov. 29 Dec.      | 6 Dec. 10 Feb.     | 5 Jan. 1 Mar.               | 23 Apr. 25 Apr. | 65 63     | 108 55     |
| 2003/2004      | Akitakko        | 5 Nov. 26 Jan.      | 17 Feb. 2 Mar.     | 14 Mar. 19 Mar.             | 28 Apr. 28 Apr. | 130 53    | 45 40      |
|                | Iwainodaichi    | 26 Oct. 2 Jan.      | 16 Dec. 5 Feb.     | 4 Jan. 26 Feb.              | 20 Apr. 21 Apr. | 70 55     | 107 55     |
|                | Airakomugi      | 25 Oct. 3 Jan.      | 7 Dec. 8 Feb.      | 18 Dec. 27 Feb.             | 20 Apr. 21 Apr. | 54 55     | 124 54     |

FI, Flag leaf initiation. TS, Terminal spikelet initiation. An, Anthesis.

Fig. 3. Mean air temperature from October to April in the three growing seasons and an average year.

November, and was lower than in an average year. It then increased until April, showing almost the same temperature as in an average year except in early January when it was temporarily lower. In 2003/2004, the temperature was higher than in an average year during November, but was considerably lower than an
average year temporarily in late January, then it rose to the level in an average year, and was higher from mid-to late February and in mid-March than in an average year.

### Table 4. Results of multiple regression analysis for relationships of spikelet number per spike with the spike number and the mean air temperature from flag leaf initiation to terminal spikelet initiation.

| Treatment          | Growing season | Multiple regression equation | Significance of regression | Correlation coefficient |
|--------------------|----------------|------------------------------|----------------------------|-------------------------|
|                    |                |                              | Multiple regression        | Primary regression      | Multiple correlation coefficient | Simple correlation coefficient |
|                    |                |                              | with $x_1$                 | with $x_2$              | with $x_1$               | with $x_2$               |
| Early-sown group   | 2001/2002      | $y=0.001x_1-0.379x_2+20.91$ | $17.75^{NS}$              | $0.048^{NS}$            | $0.973^*$               | $0.125^{NS}$             |
|                    | 2002/2003      | $y=0.014x_1-2.065x_2+25.83$ | $12.91^{NS}$              | $2.929^{NS}$            | $0.963^*$               | $0.703^{NS}$             |
|                    | 2003/2004      | $y=-0.099x_1+0.173x_2+14.10$ | $4.873^*$                 | $9.104^*$              | $0.703^*$               | $0.673^*$               |
|                    | 2001~2004      | $y=-0.002x_1+0.786x_2+19.57$ | $19.15^*$                 | $16.95^*$              | $0.975^*$               | $-0.922^*$              |
|                    |                |                              |                            |                         |                         |                         |
| Standard group     | 2001/2002      | $y=-0.0002x_1+1.744x_2+10.83$ | $83.87^*$                 | $13.15^*$              | $0.994^{**}$            | $-0.992^{**}$            |
|                    | 2002/2003      |                              |                            |                         |                         |                         |
|                    | 2003/2004      |                              |                            |                         |                         |                         |
|                    | 2001~2004      | $y=0.0121x_1+2.394x_2-0.666$ | $10.95^{**}$              | $0.081^{NS}$           | $0.829^{**}$            | $-0.086^{NS}$           |

y: Spikelet number per spike. $x_1$: Spike number. $x_2$: Mean air temperature from flag leaf initiation to terminal spikelet initiation.

*, Significant at 5% level. **, Significant at 1% level. NS, Not significant.

3. Relationship of spikelet number per spike with the temperature from flag leaf initiation to terminal spikelet initiation

Fig. 4 shows the relationship between spikelet number per spike and the mean air temperature from flag-leaf to terminal-spikelet initiation. In the
standard group, spikelet number per spike showed a positive linear relation with the temperature within the range of 4°C to 8°C in each growing season. In the early-sown group, it showed a negative relationship with the temperature within the range of 6°C to 12°C, particularly in 2001/2002.

Table 4 shows the results of multiple regression analysis for the relationship of spikelet number per spike with the spike number and the mean air temperature from flag leaf initiation to terminal spikelet initiation. There was a significant negative correlation between spikelet number per spike and spike number for the standard group in 2001/2002 and 2002/2003. The early-sown group showed a positive relation of spikelet number per spike with spike number in 2002/2003, while there was no such relations in 2001/2002. Spikelet number per spike increased with the increase in spike number under high yielding conditions like those in the growing season of 2002/2003.
Table 5 shows the number of spikelet primordia differentiated before and after the double ridge stage in the early-sown and standard groups in 2001/2002 and 2002/2003. Many of the spikelets differentiated before the double ridge stage in both growing seasons. In particular, fewer primordia differentiated after the double ridge stage in the early-sown group of 2001/2002. In Iwainodaichi and Akitakko, the number of primordia differentiated after the double ridge stage was decreased, while the number differentiated before the double ridge stage was increased by early sowing in both 2001/2002 and 2002/2003.

4. Relationship of grain number per spikelet with the temperature from terminal spikelet initiation to anthesis

Fig. 5 shows the relationship between grain number per spikelet and the mean air temperature from terminal spikelet initiation to anthesis. There was no relation between grain number per spikelet and the temperature.

Discussion

Grain number per spike was decreased by early sowing in almost all cultivars throughout three growing seasons (Table 1). The spikelet number per spike was also decreased by early sowing in Hokushin, Akitakko and Nanbukomugi, which had a strong winter habit (Table 2), and the grain number per spikelet was also decreased by early sowing in Iwainodaichi and Airakomugi, which had a moderate winter habit.

The spike development stage was advanced or delayed by early sowing in Yamaguchi because early sowing changed the temperature conditions at each developmental phase. For example, the double ridge stage was on January 3 and December 28 in Iwainodaichi and Airakomugi, respectively, in 2001/2002, while it was on December 15 and December 6, respectively in 2002/2003, which were accelerated more than half a month earlier than in 2001/2002 (Table 3). In 2002/2003, the temperature from early to mid-November, which corresponds to the juvenile phase of the early-sown group, was lower than in the average year, and such coldness must have vernalized Iwainodaichi and Airakomugi, which showed a moderate winter habit. The coldness during autumn sometimes causes trouble in these cultivars under early-sowing cultivation. The successful yield in these cultivars may depend on the temperature in the spike development phase.

The spikelet number per spike in Airakomugi in the early-sown group was lower in 2002/2003 than in the other growing seasons (Fig. 2). This is because they had many small spikes with fewer grains that appeared late after the main culms perished by the severe cold. Therefore, the data of Airakomugi in the early-sown group of 2002/2003 is excluded from the following discussion.

Spikelet number per spike is determined by the number of spikelet primordia differentiated during the period from flag leaf initiation to terminal spikelet initiation. Hokushin, Akitakko and Nanbukomugi had this phase was prolonged by early sowing (Table 3), but this prolonged phase did not result in an increase in the primodium numbers (Table 5).

Reynolds et al. (2002) suggested that the growth stage of spike primordia growth stage was generally the most sensitive to environmental factors. They also reported that Durum was the most sensitive to pre-anthesis conditions, requiring higher radiation and a cooler average temperature to produce a large number of grains. Slafer and Rawson (1994) mentioned that there was a curvilinear relationship between the final spikelet number and temperature, with an optimum at about 19°C, but the temperature changed spikelet number only 3 per spike at maximum.

Differences in the winter habit of cultivars resulted in different dates of spike development stages (Table 3). This provided us different temperature conditions during the spikelet differentiated phase, allowing us to analyze the relation between the temperature during this phase and spikelet number per spike (Fig. 4). The number of spikelets per spike increased linearly as the temperature rose at a rate of 1.5 primordia per centigrade degree within the range of 4°C to 8°C in the standard group, and it decreased slightly as the temperature increased within a range of from 6°C to 12°C in the early-sown group. Cultivars which had only a moderate winter habit would have fewer spikelet numbers per spike than cultivars which had a strong winter habit in the standard group (Table 2) because their spikelet development phase was earlier and still in severe coldness (Table 3). They also had fewer spikelets per spike than those with a strong winter habit in the early-sown group, because their spikelet development phase was shorter due to the warm temperature in earlier autumn.

Yield components usually have a negative correlation with each other. Grain number per spike is also considered to have a negative relation with spike number. The spikelet number per spike was analyzed as a response variable of multiple regression with the spike number and the mean temperature as predictor variables (Table 4). The analysis showed a significant multiple correlation coefficient, suggesting that spike number is closely related with the spikelet numbers per spike. The simple correlation coefficient of the spikelet number per spike with spike number showed a significant negative correlation in the standard group, but a positive one in the early-sown group.

Early sowing is considered to increase the number of tillers in wheat plants during the warm vegetative growth phase. However spike number did not increase by early sowing even in those cultivars that had a strong
winter habit (Table 1) due to the longer vegetative growth, indicating that many of these tillers were non-productive. Fertile cultivation conditions must make these tillers productive, and thus produce many spikes and spikelets.

As mentioned above, spikelet number per spike in the early-sown group increased under cool and fertile conditions during the spikelet-differentiating period from flag leaf initiation to terminal spikelet initiation. Nevertheless, the number of spikelet primordia differentiated before and after the double ridge stage varied with the cultivar even within the cultivars that had a strong winter habit (Table 5). The double ridge stage may be thought of as just part of the spike development phase and thus may not be so important from a physiological point of view (Kirby et al., 1987; Delecolle et al., 1989). However, it is the most important stage that is useful in recognizing the turning point from the vegetative to the reproductive phase as the growing spikelet primordium become larger than the aborting bract primordium (Toyota et al., 2001). The difference between spikelet number differentiated before and after the double ridge stage varies with the cultivar, and this indicates a difference in the spike development among the cultivars. We should investigate such a difference of cultivars and its relation to spikelet numbers.

Many researchers noted the period between terminal spikelet initiation and anthesis, the phase of stem elongation, as a more significant phase for spike development rather than the others (Fischer, 1985; Slafer et al., 2001; Gonzalez et al., 2005). They tried to prolong this phase or to promote spike growth during it. Grain number per spikelet was lower in the early-sown group than in the standard group during it. Grain number per spikelet varied with the growing season. There was no clear correlation between grain number per spikelet and the temperature from the terminal spikelet initiation to anthesis (Fig. 5).

Durum wheats are the most sensitive to pre-anthesis conditions, requiring a higher radiation and a cooler average temperature to increase grain number (Reynolds et al., 2002). Grain number on wheat tillers was declined by heat stress applied before anthesis (Fischer, 1985; Wollenweber et al., 2003). In barley the number of grains was positively correlated with N and P contents of spike as well as the dry weight of spikes at heading (Prystupa et al., 2004). As these reports show, grain numbers per spikelet could be determined by spike growth conditions around pre-anthesis. The important factor might be not only meteorological conditions, such as radiation or temperature, but also field conditions, such as soil fertility that varies with the growing season. The third floret in a spikelet might also be important to determine the grain numbers per spikelet. Vascular bundles from spike axis are known to connect directly to three basal florets (Hanif and Langer, 1972). The fourth floret has a sub-bundle derived from the bundle of the third floret. Takahashi and Kanazawa (1996) showed that the lack of assimilation during the initial grain filling period made the grain of the third floret abortive or lighter. Lack of spike growth may affect the growth of the third or higher florets.

Spink et al. (2000) examined the optimum plant density in England over three years, and reported that the earlier the seed was sown in autumn, the lower the optimum density. They further showed that the reduced population was compensated by increased shoot numbers per plant, increased grain number per spike and, to a lesser extent, increased grain size. It increase the productive tillers in the early-sown group in Yamaguchi, we should examine the optimum density for the early sowing. In future, we must also determine the effect of interaction among cultivars, fertility and planting density.

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