Tillering Responses to High Red/ Far-Red Ratio of Four Japanese Wheat Cultivars

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Abstract: The effect of high red/ far-red ratio (R/FR) on tillering in wheat and its cultivar differences were investigated with a pot experiment. Four Japanese wheat cultivars with a different degree of winter habit: Abukumawase, Sanukinoyume 2000, Norin 61 and Iwainodaichi, were grown under the tunnels with different R/FR conditions: one tunnel covered with a light control film which attenuates irradiance in the far red range (high R/FR) and the other with a transparent polyethylene film with a white shading cloth (control). The high R/FR treatment increased R/FR by 25%, and slightly decreased air temperature. The low temperature in high R/FR had some effect on the time of the developmental stage; however, physiological responses to high R/FR and its cultivar differences were observed. Tillering dynamics was quantified and analyzed based on phyllochron, site-filling and the time of cessation of tillering. The high R/FR significantly delayed the time in calendar days of full expansion of flag leaf and anthesis, but the effect of treatment was not significant in growing degree days. The high R/FR had no significant effect on the phyllochron and the maximum number of leaves on the main stem. The maximum number of tillers per plant was significantly increased and the cessation of tillering was significantly delayed by the high R/FR in all cultivars. In conclusion, the increase in the number of tillers in the high R/FR was attributed mainly to the delay of the cessation of tiller emergence, along with the significant increase in rate of tillering in some cultivars.

Key words: Light quality, Phyllochron, R/FR, Site-filling, Tiller, Vernalization requirement, Wheat.

The number of spikes per unit area is one of the main yield components of wheat yield along with the number of grains per spike. The number of spikes at maturity is the product of the maximum number of emerged tillers and its survival rate. Planting density strongly affects the emergence and survival of tillers (Darwinkel, 1978) through the response to light environment.

Plants sense light through photoreceptors: phytochrome, cryptochrome and phototropin, and induces photomorphogenetic responses (Smith, 2000). A common parameter to assess the effect of light quality on plant growth and development is the red/ far-red ratio (R/FR), which is the ratio of the photon irradiance of about 665 nm (R) to that of about 730 nm (FR). R/FR of daylight is approximately 1.2, while under the plant canopy the ratio is lowered due to the absorption of red light by photosynthetic pigments. The lowered R/FR directs plants to the responses termed shade avoidance syndrome: enhanced elongation growth, accelerated flowering, increased apical dominance and decreased tiller emergence (Ballaré and Casal, 2000; Smith, 2000; Franklin and Whitelam, 2005). The cessation of tillering in wheat is induced when the fraction of photosynthetically available radiation (PAR) intercepted by the canopy exceeds a threshold (0.40 – 0.45) and R/FR drops below 0.35 – 0.40 (Evers et al., 2006), and tiller death in wheat started at R/FR of 0.2 – 0.4 (Sparkes et al., 2006). Thus, light quantity as well as light quality within a crop canopy regulates tillering dynamics, and determines the size and geometrical characteristics of a canopy.

Wheat breeding in the southwest region of Japan has increased the number of spikes per plant (Chujo et al., 1989). Tillering study with Japanese wheat cultivars bred in a different era revealed that the cultivar difference in the number of spikes per plant was due to the difference in survival rate of emerged tillers, not to that in appearance rate of tillers (Chujo et al., 1989, 1990). Li et al. (1994) reported a higher specific leaf area with thinner and longer leaf blades in dense planting than in sparse planting in wheat, and they speculated that the R/FR ratio would affect these morphological characters. However, little has been reported.
on the tillering responses to R/FR in Japanese wheat.

Furthermore, the yield of early wheat cultivars (cultivar with low vernalization requirement) in southwestern regions of Japan are prone to decrease and unstable in warm-winter year due to the reduction of spike number caused by the shortening of tillering period (Taya, 1993; Fujita, 1997; Seki et al., 2007). Therefore, the influence of the vernalization requirement of cultivars on tillering responses by light environment should be explored.

The objective of this study is to quantify the effect of R/FR on the tillering response of wheat, and to analyze whether the effect varies with the cultivar among the four Japanese wheat cultivars, which have different degrees of winter habit.

Materials and Methods

1. Plant materials

A pot experiment was conducted at the Faculty of Agriculture, Kagawa University (N34°16'17", E134°7'39") from the autumn of 2006 to the spring of 2007. Four Japanese wheat cultivars with different degrees of winter habit were used: Abukumawase, which has no or very low vernalization requirements (Degree of winter habit I), Sanukinoyume 2000 and Norin 61, which have low vernalization requirements (Degree of winter habit II), and Iwainodaichi, which has moderate vernalization requirements (Degree of winter habit IV). Three seeds per pot were sown on 14 November in unglazed pot (9 L) filled with a field soil. After emergence, plants were thinned to one seedling per pot. Thirty-two pots (8 pots per cultivar) were prepared and placed in open air in the field till the start of treatment. Plants were fertilized the day before sowing with 4.2 g per pot of a compound fertilizer containing 10% of N, P₂O₅ and K₂O each. Supplemental nitrogen, 0.7 g of ammonium sulfate per pot, was applied on 9 February. Pots were watered as required.

2. Treatment

The high R/FR ratio was provided by placing the pots into the tunnel (1.4 m height, 1.2 m width and 4 m length) placed in the field, which was covered with a 0.1 mm thick light control film (Megacool, MKV Platech Co., Ltd.) which attenuates irradiance higher than 660 nm. The control pots were placed into the tunnel which was covered with a 0.03 mm thick transparent polyethylene film and a white shading cloth. A white shading cloth which reduces 23% of ambient light was placed under the transparent polyethylene film to make the photosynthetic photon flux density (PPFD) approximately equal in high R/FR and control. Both ends of the films and white cloth were cut and removed about 20 cm above the soil surface for ventilation. The pots were carried into the tunnels on 18 December, and the tunnels were disassembled and removed on 6 March (79 days of light treatment). These plants were left to grow in open air in the same place until the ripening stage.

3. Measurements

The number of tillers per plant including main stem (MS) and the leaf stage of MS were measured twice a week until anthesis. The number of tillers per plant includes tillers, which may cease growth. The leaf stage was measured as the Haun stage (HS) (Haun, 1973). The phyllochron, the time intervals between appearance of successive leaves (Rickman and Klepper, 1995), was estimated from the slope of the regression line between Haun stage (HS) and growing degree-days (GDD), which is the cumulative daily mean temperature above 0°C. Regressions between HS and days after seeding (DAS) were calculated to estimate the phyllochron in DAS. However, if not otherwise specified, term “phyllochron” in this study means the phyllochron in GDD (ºCd). Air temperature at 10 cm above the soil surface of a pot was measured with thermistor sensors (Ondotori TR-71S, T&D Corp.) from 10 January to the ripening stage. The mean of two air temperatures measured in two different pots in each treatment were used for the calculation of GDD.

The number of tillers per plant plotted against DAS until the maximum number of tillers follows a sigmoidal curve, so that the Richards function (Richards, 1959) was applied to the relationship:

\[
Tiller\ number\ per\ plant = A[1 + e^{(b-x)/n}]^{-1/n}
\]

where \(A\) is the asymptotic maximum number of tillers per plant, \(e\) is the base of natural logarithm, and \(n\), \(b\) and \(k\) are model parameters. Theoretically, the number of tillers per plant will never reach its asymptotic maximum, so that the DAS at the 95% of \(A\) was regarded as the time of the secession of tiller emergence.

Tillering dynamics of gramineae crop is quantifiable with leaf appearance rate expressed as phyllochron and site-filling; the increase rate of tillers per phyllochron (Davies, 1974; Neuteboom and Lantinga, 1989; Bos and Neuteboom, 1998).

Site-filling (Fs) is determined as:

\[
Fs = (\ln T_2 - \ln T_1) / (t_2 - t_1)
\]

where \(T_1\) and \(T_2\) are the number of emerged tillers per plant including MS at the time of \(t_1\) and \(t_2\) expressed as HS. In this study, Fs was calculated from the relation between the number of tillers per plant expressed on a natural logarithm scale and HS (Gautier et al., 1999). Because the regression curve of the relation (see Fig. 5) was a broken-stick shape, consisting of two lines a piecewise regression model (Toms and  Lesperance, 2003) was fitted:

\[
\ln (number\ of\ tillers\ per\ plant) = \begin{cases} 
 b + F_{S1}x, & (x \leq a) \\
 b + F_{S1}a + F_{S2} (x-a), & (x > a) 
\end{cases}
\]

where \(x\) is HS, \(b\) is intercept of the model, \(F_{S1}\) and \(F_{S2}\) are the slope of the lines, i.e., site-filling before and after the break point \(a\), respectively. The NLIN procedure of SAS.
(SAS Institute, 1995), was used for the non-linear fits of the Richards function and the piecewise regression model. The fitting of Richards function was performed to the data pooled in each cultivar and treatment, whereas the piecewise regression model was used for each plant.

The spectral photon distribution of the light was measured with a spectroradiometer (LI-1800, Li-Cor, Inc.) at midday in fine weather, 14 January. Data are means of six measurements. Vertical shaded bars indicate the ranges of red (R: 655 to 665 nm) and far-red (FR: 725 to 735 nm) wavelength.

**Results**

1. **Spectral photon distribution and temperature**

The spectral photon distributions of sunlight measured outside of the tunnel (open air) and in the tunnels covered with the light control film (High R/FR) or the transparent polyethylene film with a white shading cloth (Control) at midday of a fine weather, 14 January are shown in Fig. 1. The photon density of high R/FR was low in the range of about 300 to 500 nm and above 650 nm. The difference in photon density between the R/FR treatment and control was gradually widened with increasing wavelength above 650 nm. The high R/FR treatment decreased PPFD by 5% and significantly increased R/FR by 25% (Table 1). The daily mean air temperature in both treatments during the light treatment except for the period from 18 December to 10 January, is shown in Fig. 2. The mean daily mean air temperature for the period was 10.5 in the control and 9.7ºC in high R/FR plots; the difference was significant in six tenths of the days during the light treatment.

**2. Plant development and phenology**

At the beginning of treatment (17 December, 33 DAS), the leaf stage (HS) of main stem in Iwainodaichi and Abukumawase was 3.5 and 3.6, respectively, which were significantly higher than in Sanukinoyume 2000 and Norin 61 (Table 2). The number of tillers per plant in Sanukinoyume 2000 was 2.1, which was significantly smaller than in other cultivars.

Table 3 shows the times (DAS and GDD) of full expansion of flag leaf and anthesis, the maximum number of leaves on MS, the maximum number of tillers per plant and phyllochrons. The high R/FR delayed the time of full expansion of flag leaf by 3 days (Abukumawase and Norin 61) to 9 days (Iwainodaichi), and anthesis by 2 days (Abukumawase) to 4 days (Sanukinoyume 2000) compared with the controls. These differences corresponded to 0 ºCd

![Fig. 1.](image1.png)

**Fig. 1.** The spectral photon distributions of sunlight measured at outside of the tunnel (open air) and in the tunnels covered with the light control film (High R/FR) or the transparent polyethylene film with a white shading cloth (Control) at midday of a fine weather, 14 January. Data are means of six measurements. Vertical shaded bars indicates the ranges of red (R: 655 to 665 nm) and far-red (FR: 725 to 735 nm) wavelength.

![Fig. 2.](image2.png)

**Fig. 2.** Daily mean air temperature in the tunnels covered with the light control film (High R/FR) or the transparent polyethylene film with a white shading cloth (Control). * indicate significant difference between control and high R/FR by t-test (*n* = 2, *p* < 0.05).

| Cultivars | HS  | Tiller number per plant |
|-----------|-----|-------------------------|
| ABU       | 3.6 ± 0.04 a | 2.8 ± 0.15 a |
| SAN       | 3.3 ± 0.02 b | 2.1 ± 0.08 b |
| N61       | 3.3 ± 0.02 b | 2.9 ± 0.83 a |
| IWA       | 3.5 ± 0.02 a | 3.0 ± 0.00 a |

Means within a culm followed by the same letters are not significantly different at 5% level by Tukey’s HSD test.

ABU, Abukumawase; SAN, Sanukinoyume 2000; N61, Norin 61; IWA, Iwainodaichi.

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Table 1. Photosynthetic photon flux density (PPFD) and R/FR at midday of a fine weather, 14 January. PPFD and R/FR of sunlight outside the tunnels (open air) was shown for reference. Data are means of six measurements ± standard error.

| Treatment  | PPFD (μmol s⁻¹ m⁻²) | R/FR       |
|------------|---------------------|------------|
| Open air   | 990 ± 12            | 1.06 ± 0.002|
| Control    | 829 ± 7             | 1.03 ± 0.004|
| High R/FR  | 789 ± 2             | 1.29 ± 0.002|

*t-test*** *** indicates significant difference between the control and high R/FR at 0.1% level.

Table 2. Leaf stage (HS) of main stem and the number of tillers per plant at the start of treatment (17 December, DAS33). Data are means of 12 plants ± standard error.

| Cultivars | HS  | Tiller number per plant |
|-----------|-----|-------------------------|
| ABU       | 3.6 ± 0.04 a | 2.8 ± 0.15 a |
| SAN       | 3.3 ± 0.02 b | 2.1 ± 0.08 b |
| N61       | 3.3 ± 0.02 b | 2.9 ± 0.83 a |
| IWA       | 3.5 ± 0.02 a | 3.0 ± 0.00 a |

Means within a culm followed by the same letters are not significantly different at 5% level by Tukey’s HSD test.

ABU, Abukumawase; SAN, Sanukinoyume 2000; N61, Norin 61; IWA, Iwainodaichi.
to 45 °Cd of delay in GDD for the full expansion of flag leaf and to 27 °Cd of delay and 10 °Cd of advance for the anthesis. The effects of cultivar and high R/FR on these times in DAS were highly significant, whereas the effect of R/FR was significant in cultivar only on these times in GDD. The maximum number of leaves on MS in the control was largest in Iwainodaichi and smallest in Abukumawase, and the maximum number of tillers per plant in the control was the largest in Iwainodaichi and the fewest in Sanukinoyume 2000. The maximum number of leaves in MS was not affected by high R/FR, while the maximum number of tillers per plant in high R/FR was increased by 13% (Norin 61) to 23% (Abukumawase). The effect of cultivar was significant both on the maximum number of leaves on MS and the maximum number of tillers per plant, whereas the effect of R/FR was significant only on the maximum number of tillers per plant.

There were highly significant relationships between HS and GDD regardless of cultivars and treatments (Fig. 3). The high R/FR significantly increased the phyllochron in DAS compared with the control in all cultivars, whereas the phyllochron in GDD was increased by a high R/FR only in Iwainodaichi and Sanukinoyume 2000, whereas the effect of a high R/FR on the phyllochron in GDD was not significant (Table 3). The phyllochron in DAS and in GDD were the highest in Abukumawase, followed by Norin 61, Sanukinoyume 2000 and Iwainodaichi in both high R/FR and control. The ranking order of phyllochron in both DAS and GDD showed inverse relationships with the maximum number of leaves in MS.

### 3. Tillering

The number of tillers per plant plotted against DAS showed asymmetric sigmoidal curves (Fig. 4). The Richards function fitted well to the relations for all cultivar and treatments; RMSE of the fitting were ranged from 0.67 to 2.61 (Table 4). The relationship between the observed (maximum number of tillers per plant in Table 3) and the estimated (95% of A in Table 4) maximum number of tillers per plant was highly significant (r = 0.994, p < 0.0001). In Iwainodaichi, the number of tillers in high R/FR tended to be smaller than in the control from about 45 to 90 DAS (Fig. 4 d), and reached the estimated maximum number of tillers (95% of A) at 8 days earlier than in the control (Table 4). The observed maximum number of

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**Table 3. Effects of high R/FR on the time (DAS or GDD) of full expansion of flag leaf and anthesis, and on the maximum number of leaves on MS, the maximum number of tillers per plant and phyllochrons in four Japanese wheat cultivars.**

| Cultivars | Treatment | Full expansion of flag leaf | Anthesis | Maximum number of leaves in MS | Maximum number of tillers per plant | Phyllochron |
|----------|-----------|---------------------------|----------|-------------------------------|-------------------------------------|-------------|
|          |           | DAS | GDD | DAS | GDD |                                 | d leaf⁻¹ | ºCd leaf⁻¹ |
| ABU      | Control   | 109 | 560 | 139 | 895 | 9.3 | 22.8 | 14.6 | 155 |
|          | High R/FR | 112 | 560 | 141 | 885 | 9.3 | 28.0 | 14.9 | 148 |
| SAN      | Control   | 123 | 698 | 147 | 996 | 10.0 | 21.0 | 12.5 | 132 |
|          | High R/FR | 131 | 740 | 151 | 1023 | 10.0 | 24.3 | 13.5 | 134 |
| N61      | Control   | 129 | 752 | 149 | 1041 | 10.0 | 25.0 | 13.7 | 145 |
|          | High R/FR | 132 | 752 | 152 | 1046 | 10.3 | 28.3 | 14.4 | 143 |
| IWA      | Control   | 120 | 670 | 146 | 983 | 11.0 | 29.0 | 11.4 | 120 |
|          | High R/FR | 129 | 715 | 149 | 998 | 10.8 | 33.3 | 12.4 | 123 |

Cultivar (C) *** *** *** *** *** *** *** ***
Treatment (T) *** ns *** *** *** *** *** ***
C × T ns ns ns ns ns ns ns ns

Maximum number of tillers includes MS. ***, **, *: significant at 0.1%, 1% and 5% level, respectively. ns: not significant at 5% level.
ABU, Abukumawase; SAN, Sanukinoyume 2000; N61, Norin 61; IWA, Iwainodaichi.

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**Fig. 3.** HS of main stem in four wheat cultivars grown under different light conditions. Open and closed symbols indicate control and high R/FR treatment, respectively.
Abukumawase among cultivars (Table 4). On the other hand, the increase in the observed maximum number of tillers due to high R/FR was the largest (23%) in Abukumawase among cultivars (Table 3).

Fig. 5 shows the relationship between the number of tillers per plant expressed on a natural logarithm scale and HS. All relations showed a broken-stick shape. The site-tillers in Iwainodaichi in high R/FR was 15% larger than in the control (Table 3). In Sanukinoyume 2000 and Norin 61, though the effect of high R/FR on the number of tillers was unclear (Fig. 4 b, c), the time of the estimated maximum number of tillers (95% of $A$) in high R/FR was 8 and 4 days later than in the control (Table 4), resulting in 16% and 13% increase in the maximum number of tillers in Sanukinoyume 2000 and Norin 61, respectively (Table 3). In Abukumawase, the number of tillers after 60 DAS was slightly larger in high R/FR (Fig. 4 a), and the time of the estimated maximum number of tillers (95% of $A$) was 3 days later than in the control (Table 4). Thus the difference in the days required to attain the estimated maximum number of tillers between high R/FR was the shortest in

![Fig. 4](image1.png) ![Fig. 5](image2.png)

**Table 4.** The estimated maximum number of tillers per plant (95% of $A$) and the time (DAS) required to attain 95% of $A$ estimated by the Richards function, and the RMSE of fitting.

| Cultivars | Treatment | 95% of $A$ | DAS at 95% of $A$ | RMSE |
|-----------|-----------|------------|------------------|------|
| ABU       | Control   | 19.9       | 91               | 1.10 |
|           | High R/FR | 26.7       | 94               | 1.28 |
| SAN       | Control   | 19.0       | 93               | 0.67 |
|           | High R/FR | 22.5       | 101              | 1.22 |
| N61       | Control   | 23.3       | 94               | 0.93 |
|           | High R/FR | 26.5       | 98               | 2.61 |
| IWA       | Control   | 27.8       | 92               | 1.51 |
|           | High R/FR | 31.5       | 100              | 2.00 |

ABU, Abukumawase; SAN, Sanukinoyume 2000; N61, Norin 61; IWA, Iwainodaichi.

**Table 5.** Effects of high R/FR on the site filling of four Japanese wheat cultivars estimated by the piecewise regression between the number of tillers per plant (log scale) and HS.

| Cultivars | Treatment | $F_s$ 1) | $F_s$ 2) | $a$ 3) |
|-----------|-----------|----------|----------|--------|
| ABU       | Control   | 0.492    | 0.034    | 7.41   |
|           | High R/FR | 0.552    | 0.059    | 7.45   |
| SAN       | Control   | 0.529    | 0.042    | 7.58   |
|           | High R/FR | 0.560    | 0.057    | 7.73   |
| N61       | Control   | 0.586    | 0.030    | 7.02   |
|           | High R/FR | 0.559    | 0.034    | 7.41   |
| IWA       | Control   | 0.543    | 0.034    | 7.58   |
|           | High R/FR | 0.535    | 0.045    | 7.76   |

**ABU, Abukumawase; SAN, Sanukinoyume 2000; N61, Norin 61; IWA, Iwainodaichi.**

**Table 5.** Effects of high R/FR on the site filling of four Japanese wheat cultivars estimated by the piecewise regression between the number of tillers per plant (log scale) and HS.

| Cultivars | Treatment | $F_s$ 1) | $F_s$ 2) | $a$ 3) |
|-----------|-----------|----------|----------|--------|
| ABU       | Control   | 0.492    | 0.034    | 7.41   |
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| SAN       | Control   | 0.529    | 0.042    | 7.58   |
|           | High R/FR | 0.560    | 0.057    | 7.73   |
| N61       | Control   | 0.586    | 0.030    | 7.02   |
|           | High R/FR | 0.559    | 0.034    | 7.41   |
| IWA       | Control   | 0.543    | 0.034    | 7.58   |
|           | High R/FR | 0.535    | 0.045    | 7.76   |

**Cultivar (C) ** ns ** ns ** ** |
**Treatment (T) ns ns ns ** |
**C × T ** ns ns ns ns **

**, *: significant at 1% and 5% level, respectively.
ns: not significant at 5% level.
1) Site filling before ($F_s$) and after ($F_s$) the break point ($a$).
2) ABU, Abukumawase; SAN, Sanukinoyume 2000; N61, Norin 61; IWA, Iwainodaichi.

Abukumawase among cultivars (Table 4). On the other hand, the increase in the observed maximum number of tillers due to high R/FR was the largest (23%) in Abukumawase among cultivars (Table 3).

Fig. 5 shows the relationship between the number of tillers per plant expressed on a natural logarithm scale and HS. All relations showed a broken-stick shape. The site-
fillings before (F$_{1}$) and after (F$_{2}$) the break point ($a$) were estimated by fitting piecewise regression models and results were shown in Table 5. The F$_{1}$ ranged from 0.492 to 0.586, the F$_{2}$ ranged from 0.030 to 0.059. The effect of high R/FR on F$_{1}$ and F$_{2}$ are not significant, whereas the effects of cultivar and the interaction of cultivar and high R/FR on F$_{1}$ were significant. The F$_{1}$ was higher in Norin 61 in the control and high R/FR. As the interaction of cultivar and high R/FR on F$_{1}$ was significant, we tested the differences in F$_{1}$ between cultivars and between control and high R/FR. The F$_{1}$ in high R/FR was significantly higher ($p < 0.05$) than in the control in Sanukinoyume 2000 and Abukumawase, but not in Iwainodaichi and Norin 61. The cultivar differences in F$_{1}$ were significant ($p < 0.01$) in the control, but not in high R/FR. The time of break point which may represent the cessation of tiller emergence, ranged from 7.02 to 7.76. The high R/FR delayed the time of break point in all cultivars by 0.5% (Abukumawase) to 5.6% (Norin 61).

**Discussion**

1. **Experimental system**

   The light control film decreased the PPFD in the range of about 300 to 500 nm and above 650 nm (Fig. 1). As a result, the light control film significantly increased R/FR by 25%, compared with the double layer of a transparent film with a white shading cloth used as the control but at the same time it decreased PPFD by 5% (Fig. 1, Table 1). Though it is unclear whether the reduced PPFD in high R/FR affected the results of this study, the influence of reduced PPFD should be limited because the reduction rate was low (5%). The daily mean air temperature in high F/FR was approximately 0.7ºC lower than in the controls, and differences between the control and high R/FR was significant in six tenths of the days during the light treatment (Fig. 2). Therefore, the effect of the small difference of temperature between control and high R/FR should not be excluded. The effect of lowered temperature in the high R/FR on the plant development is discussed below.

2. **Plant development and phenology**

   Our results revealed that the high R/FR significantly delayed the time of full expansion of flag leaf and anthesis in calendar days (DAS) but not in GDD (Table 3). Thus, the lower daily mean temperature in high R/FR (Fig. 2) would be responsible for the delay of the time in calendar days. However, the cultivar difference in the responses to the low temperature were inconsistent with that we speculate from the degree of winter habit of these cultivars. Earlyness of the flowering in wheat depends on vernalization requirement, photoperiod response and earliness per se (Laurie et al., 2004). In general, early wheat cultivars in southwestern Japan are insensitive to photoperiod, therefore the development will be earlier in a warm-winter year than in a usual year, resulting in a frequent occurrence of frost damage due to early jointing (Taya, 1995; Fujita, 1997; Seki et al., 2007). Iwainodaichi was developed by genetic improvement of the vernalization requirement for early maturing to avoid tiller frost through the stability of jointing (Fujita, 1997). Therefore, the developmental progress in Abukumawase, which has no vernalization requirement should be delayed and in Iwainodaichi, which has moderate vernalization requirement should be less affected. However, we obtained opposite results: the delay of the full expansion of flag leaf and anthesis was less in Abukumawase than in Iwainodaichi.

   Not only temperature but also light quality affects plant development. Low R/FR condition accelerates flowering through the light quality-sensing pathway mediated by phytochromes to regulate the floral activator FT (Ballaré and Casal, 2000; Smith, 2000; Franklin and Whitelam, 2005; Thomas, 2006; Kebrom and Brutnell, 2007). Although the developmental stages in high R/FR were delayed by the low temperature to some extent, the physiological responses to R/FR ratio and its cultivar differences would be involved in the results. Furthermore, the delay of the developmental stages in high R/FR was larger in a moderate winter habit cultivar which has vernalization requirement and photoperiodic sensitivity (Iwainodaichi), and smaller in an extremely early and photoperiod insensitive cultivar (Abukumawase). These results suggested that cultivar differences in the phenological responses to R/FR could be associated with the photoperiodic sensitivity.

   The effect of high R/FR on the phyllochrons was significant in DAS and not in GDD (Table 3). Because the phyllochron in DAS includes the effect of daily mean temperature between the treatments, following discussion is based on the phyllochron in GDD to eliminate the effect of temperature.

   The high R/FR did not affect the maximum number of leaves on MS and phyllochron (Table 3). Although the high R/FR decreased phyllochron in Abukumawase by 4.5% compared with the control, the effect of R/FR on phyllochron in other cultivars was slight. The inverse relationship between the phyllochrons and the maximum number of leaves on MS (Table 3) suggested that the cultivars with lower vernalization requirement tended to have larger phyllochron and fewer maximum leaf number on MS.

   Thus our results indicated that high R/FR delays the time of flowering, but does not affect the number of leaves on the main stem and phyllochron.

3. **Tillering**

   The high R/FR increased the maximum number of tillers per plant in all cultivars by 13% (Norin 61) to 23%
(Abukumawase) compared with the control (Table 3). The tillering responses to high R/FR and its cultivar differences are discussed with regard to phyllochron, site-filling and the time of cessation of tillering.

In Abukumawase, which showed the largest increase in the number of tillers in high R/FR, the delay of the time attaining the maximum number of tillers (Fig. 4 a, Table 4) and that of the time of break point (Fig. 5 a, Table 5) in high R/FR were the smallest among cultivars. Conversely, the effect of high R/FR on the phyllochron and the site-filling before the break point were the largest in Abukumawase among cultivars: the phyllochron was decreased by 4.5% (Table 3), and FS was increased by 12.2% in high R/FR (Table 5). Therefore, the great increase in the number of tillers in high R/FR in Abukumawase is attributed mainly to the early leaf emergence on MS and the high rate of tiller production rather than the delay of the cessation of tiller emergence.

In Iwainodaichi, on the other hand, the delay of the time attaining the maximum number of tillers in high R/FR was the greatest (8 days) among cultivars (Table 4). In Iwainodaichi, phyllochron was increased by high R/FR 2.5% and FS, was decreased by 1.5% compared with the control (Table 3, Table 5). Although high R/FR in Iwainodaichi slowed the rate of leaf emergence in MS and tiller production, and these responses led to decrease in tillering to some extent, the delayed cessation of tiller emergence was the main factor for the increased number of tillers in high R/FR in this cultivar.

Thus, the effect of high R/FR on phyllochron in all cultivars (Table 3) and site-filling in Iwainodaichi and Norin 61 were not significant (Table 5), and the effects in phyllochron and the site-filling were either positive or negative; the effects varied with the cultivar were different with each cultivars. On the other hand, the cessation of tiller emergence were delayed by high R/FR in all cultivars.

In conclusion, the high R/FR treatment significantly increased the number of tillers per plant in all cultivars examined in this experiment without affecting the number of leaves on the main stem and the phyllochron. The increase in the number of tillers in high R/FR was attributed mainly to the delay of the cessation of tiller emergence, along with the significant increase in site-filling in some cultivars.

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