Assimilate Supply as a Yield Determination Factor in Spring Wheat under High Temperature Conditions in the Mediterranean Zone of South-East Turkey

Tohru Kobata¹, Müjde Koç², Celaleddin Barutçu³lar², Takuya Matsumoto¹, Hiroshi Nakagawa³, Fumihiko Adachi¹ and Mustafa Ünlü²

¹Faculty of Life and Environmental Science, Shimane University, 1060 Nishikawatu-cho, Matsue 690-8504, Japan; ²Faculty of Agriculture, Çukurova University, 01330 Balcalı, Adana Turkey; ³National Agricultural Research Center, 3-1-1 Kannondai, Tsukuba 305-8666, Japan

Abstract: Wheat in the Mediterranean zone often encounters high temperatures during the terminal growth stage. This study investigated whether assimilate supply by source-function plays a dominant role in determining grain production in spring wheat exposed to high terminal-temperatures in the Mediterranean zone of south-east Turkey. The spring wheat cultivar Adana99 was grown under irrigated conditions sowing according to the current schedule (CS plants) and late-sowing (LS plants) for two years. Grain yield of CS plants, which were subjected to relatively lower temperatures during the terminal growth stage, was higher than that of LS plants, which were subjected to relatively higher temperatures. A high temperature in the post-anthesis period accelerated leaf senescence and reduced radiation-use efficiency. Halving the plant density at anthesis, which increases assimilate supply to grains, significantly increased the grain dry weight (GDW) and whole plant dry weight (WPDW) in the post-anthesis period. Grain filling percentage (F%, observed/final GDW) in thinned plants, which was regarded as potential F%, showed a single logistic equation based on cumulative temperature after anthesis, regardless of post-anthesis temperatures. In the LS plants, the daily increase in WPDW (ΔWPDW) decreased, but the peak of an increase rate of potential GDW estimated from F% was shifted to earlier-filling stage, resulting in reduced GDW at harvest. The final GDW in both years closely correlated with the estimated ΔWPDW in the grain-filling period. These results suggest that source-function for assimilate supply in the post-anthesis period is one of the important yield-determining processes in spring wheat subjected to high temperatures.

Key words: Assimilate supply, High temperature, Mediterranean zone, Post-anthesis period, Spring wheat, Turkey.

High temperatures promote plant development and shorten the growth period and as a result, wheat grain yield is low due to reduced plant biomass and restricted sink size (Bell et al., 1994; Egli, 1998). In the reproductive stage, exposure to high temperatures substantially reduces the grain yield by reducing grain set and grain size (Bell et al., 1994; Egli, 1998). In the Mediterranean area, spring wheat grows under relatively cool and moist conditions in the early growth period and is often exposed to high temperatures, temporary heat shock and drought in the terminal growth stage such as the grain-filling period (Nicolas and Turner, 1996; Evans, 1996; Turner, 1997; Savin et al., 1999). High temperatures and drought in the terminal stage can critically damage grain production in the rain-fed wheat of the area, while temperature can also have an adverse effect on irrigated wheat (Ortiz-Monasterio et al., 1994). Furthermore, future negative impact of global warming on wheat production in agricultural zones of the Mediterranean region is a concern (Evans, 1996; Asseng et al., 2004). In Adana, an area important for wheat production in the south-east Mediterranean zone of Turkey, the average temperature has been increasing at a rate of 0.01°C per year since 1930 and the annual rainfall has been decreasing at a rate of 7 mm per year since 1980 (DMI, 2005). In the last part of this century, the average temperature in this area is predicted to have increased by 2–3.5°C and the annual rainfall to have decreased by 25% from the current annual rainfall (Kimura, 2007). Hence,
the impact of a high temperature and water shortage on wheat production in this area is of concern now and more so in the future.

High temperature and drought in the terminal growth stage of wheat have serious negative effects on grain yields through their effects on yield components such as floret number, fertility, number of set grains and individual grain weight (Barrow et al., 1980; Wardlaw, 1994; Turner, 1997; Calderini et al., 1999; Egli, 2004; Ugarte et al., 2007). However, high temperatures and water deficit have different effects on grain growth in wheat. The increase per day of grain dry weight (GDW) is suppressed by water deficit, mainly due to failure of the source function, such as the inhibition of assimilation processes (Kobata et al., 1992; Palta et al., 1996; Turner, 1997). As evidence that the suppressed increase rate of GDW \( \Delta \text{GDW} \) results from suppression of the source function, if assimilate supply is secured by another alternative assimilate source such as stem reserved carbohydrate, grain growth can be maintained under water deficit conditions in wheat (Wardlaw, 1968) and other crops such as maize (Boyer and McPherson, 1976) and rice (Kobata and Takami, 1979).

A high temperature accelerates the increase in GDW, but shortens the grain-filling period, resulting in a yield reduction, that is, acceleration of the increase in GDW cannot compensate for the shortening of the grain-filling period (Sofield et al., 1977; Wardlaw et al., 1980; Tashiro and Wardlaw, 1989; Tashiro and Wardlaw, 1990; Wheeler et al., 1996). A similar phenomenon has been observed in other grain crops such as rice (Sato and Inaba, 1976; Tashiro and Wardlaw, 1989), barley (Wallwork et al., 1988), maize (Jones et al., 1981) and soybeans (Egli and Wardlaw, 1980; Gibson and Mullen, 1996). Hence, it is suggested that the lower GDW under high-temperature conditions is due to failure of the sink function, such as the loss of enzyme activity in the grains (Jenner, 1991; Hawker and Jenner, 1993; Zahedi et al., 2003) or a reduced grain capacity, due to decreased endosperm cell size in wheat (Hoshikawa, 1961), barley (Wallwork et al., 1998) and rice (Sato and Inaba, 1976; Morita et al., 2005). Therefore, the reduction of the GDW through high temperatures is considered to be mainly caused by a failure of the sink function, although the reduction by water deficit results mainly from a failure of the source function.

However, in rice, the source function in grain production is more important than the sink function not only under water deficit (Kobata and Takami, 1979) but under high-temperature conditions (Kobata and Uemuki, 2004; Kobata et al., 2004). In field-grown rice, high temperatures during the grain-filling period increased the \( \Delta \text{GDW} \) and shortened the grain-filling period, but the final grain dry weight (GDW) did not decrease when assimilation after anthesis was increased by thinning treatments (Kobata and Uemuki, 2004; Kobata et al., 2004). Therefore, the potential \( \Delta \text{GDW} \) (\( \Delta \text{PGDW} \)) in rice should be little inhibited by high temperatures, but failure of the assimilate supply to grains to meet the requirements of the accelerated \( \Delta \text{GDW} \) plays a dominant role in the decrease in GDW under post anthesis high-temperature conditions. Moreover, under high-temperature conditions, assimilate supply to the grains is reduced due to increased respiration (Amthor, 1989) and accelerated leaf death (Begg, 1980). In fact, the importance of the advanced effects of assimilate supply on the reduction of GDW under high temperature and water deficit conditions have been observed (Nicolas et al., 1984; Wardlaw, 1994).

Most of the effects of high temperature on grain growth in wheat have been studied on the grains at specific positions such as the predominant grains in the central position of the spike in isolated plants or single culm plants grown in pots in controlled growth chambers (Sofield et al., 1977; Tashiro and Wardlaw, 1989), except for a few cases (Savin et al., 1999). Assimilate supply in isolated plants such as potted plants would be less limited than that in crop plants, because isolated plants can receive abundant irradiance but crop plants in the field sometimes suffer from a shortage of assimilate supply due to the mutual shading of plants (Evans, 1996; Egli, 1998), and hence the contribution of assimilate supply to grains is more likely to be underestimated in isolated plants compared with crop plants. Furthermore, the effect of temperature on grains should be evaluated for the grains on whole plant spikes and not for those at specific positions such as central spikelets because the GDW in response to temperature may differ with the position of the grain, predominant central and non-predominant distal grains, and because the grain yield is determined by both individual grain weight and grain number. However, the importance of source functions such as assimilate supply compared with sink functions in the plants subjected to high temperatures under field conditions has rarely been studied.

The aims of this study were to evaluate the effect of assimilate supply on grain growth in irrigated spring wheat that were subject to high temperatures in the Mediterranean zone in south-east Turkey, and to test if the shortage of assimilate supply to grains exposed to higher temperatures critically reduces the grain yield.

**Materials and Methods**

1. **Site, experimental design and crop management**

Field experiments were conducted at the Çukurova University experimental farm (37° N and 20° E; 43 m above sea level) in Adana, Turkey in two successive years. The soil was montmorillonitic, thermic, Vertic Xerofluvent with low organic matter and pH ranged between 7.05 and 7.20. The amounts of fertilizer provided were 200 kg N ha\(^{-1}\) as NH\(_4\)NO\(_3\), 80 kg P ha\(^{-1}\) as P\(_2\)O\(_5\), 80 kg K ha\(^{-1}\) as K\(_2\)O
Plant density was halved at anthesis to increase assimilate supply to grains during the grain-filling period (Fischer and Laing, 1976; Kobata et al. 2000; Kobata and Uemuki, 2004; Kakiuchi and Kobata, 2004). In the thinning plot, plants were thinned to every other row at anthesis in irrigated plots. The experimental design was a randomised block replicated four times in both years. Experimental plots consisted of four treatments in each year: two cropping seasons (current and late sowings) × two planting densities after the anthesis period (standard and thinning). The least squares method was used to fit a logistic curve of F% plotted against the cumulative temperatures, and the decision coefficient was calculated to assess the goodness of fit of the curve. Average temperature of each day was cumulated for the pre- and post-anthesis period where zero was used as the constant value of base temperature, because it was between 0.5 and 3.9°C in spring wheat (van Keulen and Seligman, 1987). Ambient temperature, rainfall and other meteorological data were measured and logged with a data logger in a weather station adjacent to the field site.

Daily absorbed radiation was calculated from multiplying short wave radiation by radiation absorption rate (α). The α for each measurement interval was estimated from the equation by Goudriaan and van Laar (1994) for wheat: 

\[
\alpha = 1 - \exp(-k \times LAI)
\]

where \(k\) is absorption coefficient.

3. Measurements and analysis

Above-ground plant parts covering 0.3–0.5 m² per plot were harvested every 9–11 d from sowing until physiological maturity in 2005, but only two or three times after anthesis in 2004. The flowering date was defined as the date when 50% of the tillers flowered. Physiological maturity was defined as the date when 50% of the peduncles were yellow, and the glumes and grains were also losing their colour (Bell and Fisher, 1994). After leaf area of the plants was measured for leaf area index (LAI), the plants were divided into straw and spike, dried in an oven at 80°C for 48 h and weighed. Plant dry weights were determined for three parts: the grain, straw (leaf plus stem) and the whole plant (grain plus straw). Two weeks after physiological maturity was reached, 0.5 m² of plants from each replication were harvested and their yield and yield components were measured. Grains in the center of the spike (advanced grains) and distal grains of spike samples were collected separately in the second year. The former was sometimes used to monitor the effect of temperature on the grain weight because these grains can be sampled with certainty, due to high grain set, and exhibit more dominant growth than the distal grains in upper or lower parts of the spike (Bremmer and Rawson, 1978; Egli, 1998). The advanced grains were two basal grains of each spikelet in the middle part of the spike, and distal grains were all remaining grains attached to the upper and basal parts of the spikes. The significance (0.05 or 0.01 level) of differences in the yield and yield components was calculated using analysis of variance.

The grain filling percentage (F%) was defined as the ratio of the observed GDW to the potential GDW (PGDW).

\[
F\% = \left(\frac{GDW}{PGDW}\right) \times 100
\]

where PGDW is calculated by multiplying the grain number by the maximum average individual GDW in thinned plants at maturity. The least squares method was used to fit a logistic curve of F% plotted against the cumulative temperatures, and the decision coefficient was calculated to assess the goodness of fit of the curve. Average temperature of each day was cumulated for the pre- and post-anthesis period where zero was used as the constant value of base temperature, because it was between 0.5 and −3.9°C in spring wheat (van Keulen and Seligman, 1987). Ambient temperature, rainfall and other meteorological data were measured and logged with a data logger in a weather station adjacent to the field site.

1. The effect of sowing times on plants

1.1. Meteorological condition, plant growth and yield

Daily temperature increased from sowing to maturity in both years although the increase was larger in LS plants than in CS plants (Fig. 1). The mean temperature from sowing to physiological maturity in the CS and LS plants was 13.8 and 18.4°C in 2004 and 12.3 and 17.7°C in 2005, respectively. The mean temperature before anthesis in the CS and LS plants was 12.3 and 17.0°C in 2004 and 10.8 and 15.5°C in 2005, respectively and that after anthesis was 19.4 and 23.0°C in 2004 and 17.5 and 22.5°C in 2005, respectively. Thus, the average temperature in LS was 4.6 to 5.4°C higher than that in CS across the whole growing season. The cumulative radiation from seedling emergence to
Table 1. Yield and yield components in spring wheat cv. Adana99 of current and late sowing times under irrigated conditions in Adana, Turkey.

<table>
<thead>
<tr>
<th></th>
<th>Grain yield (g m(^{-2}))</th>
<th>Single grain weight (mg)</th>
<th>Grain number (m(^{-2}))</th>
<th>Biomass (g m(^{-2}))</th>
<th>Harvest index</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>2004</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Current sowing</td>
<td>564</td>
<td>28.5</td>
<td>19927</td>
<td>1668</td>
<td>0.339</td>
</tr>
<tr>
<td>Late sowing</td>
<td>533</td>
<td>31.6</td>
<td>16873</td>
<td>1560</td>
<td>0.342</td>
</tr>
<tr>
<td>Late/Current sowing</td>
<td>0.94</td>
<td>1.11</td>
<td>0.85</td>
<td>0.94</td>
<td>1.01</td>
</tr>
<tr>
<td><strong>Sowing</strong></td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>*</td>
</tr>
<tr>
<td><strong>2005</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Normal sowing</td>
<td>599</td>
<td>37.2</td>
<td>16096</td>
<td>1691</td>
<td>0.356</td>
</tr>
<tr>
<td>Late sowing</td>
<td>489</td>
<td>26.5</td>
<td>18466</td>
<td>1838</td>
<td>0.266</td>
</tr>
<tr>
<td>Late/Current sowing</td>
<td>0.82</td>
<td>0.71</td>
<td>1.15</td>
<td>1.09</td>
<td>0.75</td>
</tr>
<tr>
<td><strong>Sowing</strong></td>
<td>***</td>
<td>***</td>
<td>ns</td>
<td>ns</td>
<td>*</td>
</tr>
<tr>
<td><strong>Year</strong></td>
<td>ns</td>
<td>*</td>
<td>ns</td>
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<td>*</td>
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<tr>
<td><strong>Sowing × Year</strong></td>
<td>ns</td>
<td>***</td>
<td>*</td>
<td>ns</td>
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</tr>
</tbody>
</table>

Each value is mean for four replications. *, ** and *** indicates significant effect of level of 0.05, 0.01 and 0.001, respectively. ns is no-significant.

Fig. 1. Average temperature, fraction of transpirable soil water (FTSW), leaf area index (LAI) and whole plant dry weight (WPDW) during the growing season of spring wheat cv. Adana99 sown at current (CS) and late sowing (LS) times in 2004 and 2005 under irrigated conditions in Adana, Turkey. FTSW indicates the relative soil water content (FTSW=1 was defined as the field capacity and 0 permanent wilting point). Lateral bar in the lowest graph indicates emergence, 50% anthesis and physiological maturity sequentially from the left (▼: current sowing and ▽: late sowing). Data for dry weight is the mean ± standard error of four replications.
physiological maturity in CS and LS plants was 1305 and 1274 MJ m\(^{-2}\) in 2004 and 1095 and 1014 MJ m\(^{-2}\) in 2005, respectively and that after anthesis was 743 and 660 MJ m\(^{-2}\) in 2004 and 684 and 687 MJ m\(^{-2}\) in 2005, respectively. The trends of less radiation in the late sowing time resulted from shortening of growth duration. The duration from sowing to flowering and from flowering to physiological maturity was 58–75 days and 5–10 d, respectively, shorter in LS plants than in CS plants (Fig. 1). FTSW was maintained over 0.8 by irrigation during the whole growing season in both years although it was decreased to 0.4 at maturity in the late sowing in 2004 (Fig. 1). The whole-plant dry weight (WPDW) in the LS plants stopped increasing earlier than in the CS plants in both years, and it was lighter than in CS plants at maturity (Fig. 1).

2. The effects of temperature on grains and whole plants at maturity

The grain yield in LS plants was 6–18% lower than that in CS plants although the difference was significant only in 2005 (Table 1). Individual GDW in 2005 was significantly lighter in LS plants than in CS plants, although the difference was not significant in 2004. There were no clear difference in grain number between LS and CS plants in both years, but the interaction between sowing time and year was significant. Final WPDW at maturity varied neither with the sowing time nor the year. There was a significant difference in harvest index between LS and CS plants in both years. The harvest index was slightly (1%) higher in LS than in CS plants in 2004, but much lower (25%) in LS than in CS plants in 2005. Thus, the yield and some yield components were lower in LS plants than in CS plants in both years, although the difference was larger in 2005.

The effect of temperature in the post-anthesis period on yield components, WPDW and harvest index was assessed using the combined data of 2004 and 2005 (Fig. 2). The grain yield (g m\(^{-2}\)) and individual GDW decreased with the increase in average temperature. The individual GDW steeply decreased around 20°C. The grain number was the highest at around 18°C. The WPDW at maturity did not change with an increase in the average temperature (Fig. 2). Harvest index slightly decreased with an increase in the temperature. However, these effects of the post-anthesis temperature include the effects of other environmental factors in the pre- and post-anthesis period.

3. The effect of temperature on LAI and radiation use in different sowing times

The LAI of both years increased to 8 in the CS plants and to 6–7 in the LS plants at anthesis and then decreased (Fig. 1). The relative LAI (percentage of LAI at anthesis) of both sowing times and years increased with an increase in cumulated temperature in the pre-anthesis period while...
that in the LS plants attained the maximum LAI at lower cumulated temperature than the CS plants (Fig. 3). In the post-anthesis period the relative LAI in both CS and LS plants similarly decreased and reached zero at 800°C (Fig. 3).

In the pre-anthesis period, the WPDW linearly increased with the increase in absorbed radiation when data of CS and LS plants in both years were combined, and the radiation use efficiency (RUE) indicated by the slope of the line was 1.42 g MJ⁻¹ (Fig. 4). However, in the post-anthesis period, data points in the relationship between WPDW and absorbed radiation dispersed, and when the relationship was drawn for CS and LS, WPDW plotted against absorbed radiation in the post-anthesis period was lighter in the LS plants than in the CS plants (Fig. 5). In the regression, data for cumulated temperature less than 600°C were used, because GDW increase almost stopped at less than 600°C in both CS and LS plants and hence the temperature above that scarcely contributed to the grain-filling (Fig. 8). The RUE in the post-anthesis period was 1.91 g MJ⁻¹ in CS and 1.37 g MJ⁻¹ in LS.

Fig. 3. Relative leaf area index (LAI) (1 at anthesis) and cumulated temperature in the pre-anthesis and the post-anthesis period in the current (CS) and late sowing (LS) plants in 2004 and 2005 in spring wheat cv. Adana99 in Adana, Turkey. Each value is the mean of four replications.

Fig. 4. Whole plant dry weight (WPDW) and cumulated absorbed radiation in the current (CS) and late sowing (LS) plants of spring wheat cv. Adana99 in two years. Regression line is for data in the pre-anthesis period.

Fig. 5. Whole plant dry weight (WPDW) and cumulated absorbed radiation in the post-anthesis period in the current (CS) and late sowing (LS) plants of spring wheat cv. Adana99 in two years. Regression line is for data lower than 600°C of cumulated temperature in the post-anthesis period. *indicates data over the temperature.

2. The effect of assimilate supply increased by thinning treatments on WPDW and GDW

(1) Availability of thinning treatments to increase assimilate supply to grains

By plant thinning at anthesis, WPDW and GDW during the grain-filling period were significantly increased in both
Here, WPDW in half-density plots was doubled for comparison with standard-density plots. The WPDW in thinned plots reached the maximum at the late grain-filling period around 40 d after anthesis in the CS plants and 30 d after anthesis in the LS plants. It decreased at around 50 d after anthesis in the CS plants and around 40 d after anthesis in the LS plants. Therefore, the thinning treatment was available to increase the assimilate supply to grains. The effect of thinning on the WPDW at maturity was underestimated particularly in the LS plants and hence the dry weight at maturity did not reflect the effect of thinning treatment on dry matter production in the grain-filling period.

(2) The effect on individual GDW of different positions in the spike

The ΔGDW of the advanced and distal individual grains was higher in the LS plants than in the CS plants, but the grain-filling duration in the LS plants was shorter, resulting in a lower individual GDW in advanced and distal grains at maturity (Fig. 7). Thinning at anthesis decreased the difference in individual GDW between the CS and LS plants (Fig. 7), but not the difference between grain positions. The individual GDW in distal grains was about 17% lighter than that in advanced grains during the grain-filling period in both CS and LS plants, even when the plant density was halved (Fig. 7). The slope of the curves of individual GDW plotted against days after anthesis in advanced and distal grains were significantly different (P<0.05) in the CS plants but not in LS plants according
The maximum individual GDW was different in advanced and distal grains, and also in the CS and LS plants (Fig. 7). Under standard planting density, the F% in LS plants was slightly higher and the ceiling was lower than that in CS plants (Fig. 8-left), where the maximum individual GDW was used to calculate F%. However, the difference in F% between advanced and distal grains almost disappeared in each sowing time. The coefficient of determination ($R^2$) in the regression curve of F% against cumulative temperature was higher (0.991) when advanced and distal grains were combined in each sowing time (Fig. 8-left). Moreover, F% of advanced and distal grains in the CS and LS plants after thinning at anthesis plotted against cumulative temperature was approximately fitted to a single logistic equation ($R^2=0.992$) (Fig. 8).

(3) The effect on GDW in whole plant
Thinning treatments increased the GDW ($gm^{-2}$) in whole plant in both CS and LS plants (Fig. 6). The maximum single GDW of 43.8 mg in CS and 34.3 mg in LS plants was used for the calculation of F% (Fig. 7). The F% at a standard density in the LS plants increased at a slightly higher rate, but stopped increasing at a lower ceiling than in the CS plants (Fig. 8-right). When the plant density was halved at anthesis, however, F% approximately fitted a single equation with high $R^2$ (0.988), hence the difference in equations between the CS and LS plants almost disappeared (Fig. 8-right).

**Discussion**

1. Inhibition of assimilate supply by high temperature

The LS plants were exposed to a 5°C higher temperature during the whole growing season than the CS plants while the temperature range after anthesis was higher than before anthesis (Fig. 1). The WPDW at anthesis in the LS plants was lower than that in the CS plants (Fig. 1). The lighter WPDW was not mainly caused by suppression of assimilation capacity but by shortening of the growth term, because the RUE of whole plant before anthesis was almost the same in CS and LS plants (Fig. 4). The plant developmental stage is determined not only by temperature but also by day length (Horie, 1994). The sensitive response of LAI to cumulated temperature in the pre-anthesis period in the LS plants more than in the CS plants may be due to shortening of the growth period under a long day length, although the photoperiodic sensitivity of Adana99 seems to be low (personal comments). Although a high temperature seems to suppress the leaf area development (Fig. 3), it would decrease LAI at anthesis resulting from shortening of the period of each leaf expansion and reduction of the size of leaves (Fig. 1). In the post-anthesis period the high temperature promoted leaf senescence, reducing LAI (Fig. 4). Furthermore, the decrease in the assimilation capacity seems to be an important factor for reducing plant dry weight in the grain-filling period, because the RUE in the LS plants was lower than that in the CS plants (Fig. 5). In the post-anthesis period a high temperature would reduce assimilate supply not only by...
reducing photosynthetically active leaf areas but by suppressed photosynthetic rate. These negative effects of high temperature on assimilation in the post-anthesis period would be a consequence of the promotion of translocation of reserved assimilates and nutrient from stem organs to grains.

2. Assimilate supply as a critical factor for GDW increase under high temperature conditions

The grain yield in the two years varied from 489 to 599 g m⁻² (Table 1). The maximum and minimum were observed in 2005 with larger temperature fluctuation than in 2004 (Fig. 1). The grain yield in LS plants was lower in 2005 in which the temperature during the post-anthesis period was higher than that in 2004 (Table 1 and Fig. 1). The decrease in grain yield by the high temperature after anthesis was mainly related to the decrease in individual GDW (Table 1 and Fig. 2).

In both central and distal grains of the spike, the individual GDW was lighter in the LS than in CS plants (Fig. 7). However, when the plant density was halved at anthesis, F% plotted against cumulative temperature was nearly the same in LS and CS plants irrespective of the position of the grain in the spike (Fig. 8). Similar trends were observed for the whole plant (Figs. 6 and 8). These results suggest that the response of potential ΔGDW to temperature under higher source supply is stable under diverse temperature conditions and hence is not inhibited by high temperatures.

However, the individual GDW, even in the plants after thinning, was lighter in the LS than in the CS plants irrespective of the position of the grains in spikes and sowing time (Fig. 7). The individual GDW at the central position of the spike was heavier than that at the distal position in both CS and LS plants (Figs. 7 and 8). This may not be attributed to the difference in assimilate supply, but to the structural property of grain position within the spike (Bremmer and Rawson, 1978; Egli, 1998). There are three possible reasons for the difference in individual GDW between CS and LS plants. The first is the suppression of endosperm development by a high temperature after anthesis; a deterioration of sink function in grains due to the inhibition of metabolic processes such as starch synthesis in grains (Inaba and Sato, 1976; Jenner, 1991; Hawker and Jenner, 1993; Egli, 1998; Zahedi et al., 2003). The second is a decrease in endosperm cell size due to high temperatures in the post-anthesis period (Hoshikawa, 1961). In wheat under high temperature condition cell number per endosperm did not change (Hoshikawa, 1961) although under drought condition it decreased (Nicolas et al., 1985). The third is the effect of temperature in the pre-anthesis period. The size of carpel or ovary in wheat determined before anthesis affects the potential individual GDW and is reduced by high temperatures for two weeks in the booting stage (Wardlaw, 1994; Savin et al., 1999; Calderini et al., 1999; Ugarte et al., 2007; Ferrise et al., 2010). The first reason is a general idea, but it is uncertain whether the inhibition of metabolic processes such as starch synthesis in grains by a high temperature is the dominant reason for small grains when assimilate supply is adequate. The grain enzyme activity and gene expression relating to the enzymes are significantly affected by the supply of assimilates (Sasaki et al., 2005). The second is unsatisfactory: the decrease in the final grain
size due to a decrease in endosperm cell sizes is doubtful because the starch granules in wheat endosperm cells could expand depending on starch accumulation (Takahashi and Kanazawa, 1996). The third is one of the most promising reasons. In our study, individual GDW in halved density plants at maturity decreased when average temperature of booting stage ($T_{boot}$) for two weeks before anthesis was higher (Fig. 9-upper). Furthermore, when the effect of temperature in the post-anthesis period ($T_{post}$) on the individual GDW ($gdw_T$) of thinned plants was corrected ($gdw_T/T_{post}$), the $gdw_T/T_{post}$ decreased with an increase in $T_{boot}$ (Fig. 9-lower). Therefore, the potential individual GDW is may be influenced by $T_{boot}$.

When the plant density was halved at anthesis, F% was approximately indicated by a single equation where the difference in equations between the CS and LS plants almost disappeared (Fig. 8). If the potential ΔGDW rate ($ΔPGDW$, g m$^{-2}$ day$^{-1}$) is defined as the ΔGDW(g m$^{-2}$ day$^{-1}$) in the thinned plants, $ΔPGDW$ is given by

$$ΔPGDW = (ΔF_p/100) \times PGDW$$  \hspace{1cm} (2) \hspace{1cm}

where $ΔF_p$% is the increase rate of the potential F% (% °C$^{-1}$) and is obtained from the differential calculus of F% in halved density plants (Fig. 8). The observed ΔGDW and $ΔPGDW$ (g m$^{-2}$ day$^{-1}$) in the post-anthesis period was compared with the estimated $ΔPGDW$ in the CS and LS plants in 2005 (Fig. 10). In the CS plants, the $ΔPGDW$ was higher than the $ΔPGDW$ up to two weeks after anthesis (Fig. 10) and as a result enough dry matter could be produced before $ΔPGDW$ attained its maximum and ΔGDW should be maintained at the same level as $ΔPGDW$ before 20 d after anthesis. In the LS plants, the peak of the $ΔPGDW$ was 2–3 d earlier and the range of the peak was narrower than that in the CS plants and the $ΔPGDW$ had already started to decrease after 10 d after anthesis. As a result, the ΔGDW could not realise the $ΔPGDW$ due to lower $ΔWPDW$. These results suggest that if $ΔWPDW$ as a main assimilate source does not correspond to the increased $ΔPGDW$ by a higher temperature, the GDW can not increase by a lack of assimilate supply.

The effect of $ΔWPDW$ in the substantial grain-filling period ($ΔWPDW_s$) on the grain yield in the CS and LS plants in both years was estimated, because the $WPDW$ at maturity (Table 1) was not reflected on that in the grain-filling period (Fig. 6). The grain yield highly correlated with the $ΔWPDW_s$ in the two years, although all $ΔWPDW$ should not contribute to the grain yield after the peak of ΔGDW (Fig. 11). Here, $ΔWPDW_s$ was estimated from $α \times R_g \times RUE$, where $R_g$ is observed radiation in the substantial grain-filling period (Fig. 1), and $α$ was

Fig. 10. Change in observed increase rate of whole plant dry weight ($ΔWPDW$) and grain dry weight ($ΔGDW$) and estimated potential $ΔGDW$ ($ΔPGDW$) after anthesis in the current (CS) and the late (LS) sowing plants of wheat cv. Adana99 in 2005. $ΔWPDW$ and $ΔGDW$ were calculated from the data in Fig. 6. Estimated $ΔPGDW$ was calculated from the equation for the grain-filling percentage (F%) in half-density plants (Fig. 8) and the potential yield [Eq. (1)].

Fig. 11. Relation between grain yield and increase rate of whole plant dry weight during the grain-filling period ($ΔWPDW_s$) in wheat cv. Adana99. The $ΔWPDW_s$ was estimated from equations in Figures 4 and 5 and observed radiation. Temperature effect on radiation use efficiency was estimated assuming that it is proportional to cumulated temperature at 30 d after anthesis.
estimated from LAI (Goudriaan and van Laar, 1994) where LAI was estimated from the relationship between relative LAI and cumulated temperature after anthesis (Fig. 3) and LAI at anthesis (Fig. 1). RUE was estimated from the data of the CS and LS plants in 2005 where the RUE was proportional to cumulated temperature at 30 d after anthesis (ACT₃₀) covering the substantial grain-filling period (RUE = −0.01ACT₃₀ + 4.08) (Figs. 1 and 6).

The grain-filling period was shifted to an earlier stage by a high temperature and a decreased assimilate supply due to leaf senescence would have a high impact on the grain dry matter increase. These results suggest that the assimilate supply during the grain-filling period is a key factor for determining the grain yield of wheat particularly in high temperature conditions.

Conclusions

We conclude that a high temperature in the post-anthesis period inhibits biomass production by promoting leaf senescence and reducing RUE, and the failure of the assimilate supply to grains plays a dominant role in lowering grain yield in spring wheat subjected to a high temperature. The increase in the capacity of photosynthesis or the storage of assimilate in the stem organ should be a strategy for high-temperature tolerance in the post-anthesis period, just as for assimilate supply to grains plays a dominant role in lowering senescence and reducing RUE, and the failure of the period inhibits biomass production by promoting leaf senescence would have a high impact on the grain dry matter increase. These results suggest that the assimilate supply during the grain-filling period is a key factor for determining the grain yield of wheat particularly in high temperature conditions.

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