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Effects of Reduction in Plant Height Induced by Chlormequat on Radiation Interception and Radiation-Use Efficiency in Wheat in Southwest Japan

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Abstract: The effects of reducing plant height by the growth retardant chlormequat on radiation interception and radiation-use efficiency in field-grown wheat were studied in southwest Japan. Chlormequat was applied to wheat cultivar Sanukinoyume 2000 at the beginning of jointing. The cumulative total solar radiation intercepted by the plant canopy (Si) was determined by continuous measurements of total solar radiation above the canopy with a dome pyranometer and below the canopy with tube solarimeters. Nondestructive measurement of leaf area index (LAI) and mean tip angle of the canopy (MTA) using a plant canopy analyzer was performed weekly. Chlormequat application shortened the culm length by 12.6% compared with the control, but did not affect the aboveground dry matter (AGDM), LAI, yield or yield components except for the harvest index (HI). The extinction coefficient in canopy (K) was not affected by chlormequat, so that Si at heading and anthesis were not significantly different. Radiation-use efficiency (RUE) of chlormequat treated plants estimated from the slope of a linear regression of Si vs AGDM was 1.34 $g MJ^{1}$ for the period up to heading and 1.57 $g MJ^{1}$ for the period up to anthesis. The RUE values were not significantly different between chlormequat-treated and control plants. Although the effect may be restricted to the duration from heading to the premature ripening stage, a higher MTA in chlormequat should provide a more even distribution of radiation within the canopy, which should increase the photosynthetic performance. These results suggested that shortening the culm length of this wheat cultivar by about 12% is beneficial in reducing the risk of lodging without affecting light interception characteristics or RUE.

Key words: Chlormequat, Dwarfing, Extinction coefficient, Mean tip angle, Radiation interception, Radiation-use efficiency, Wheat.

Reducing culm length in wheat prevents lodging and reduces intra-shoot (spike vs culm) competition for assimilates. Both impacts are beneficial for increasing grain yield, and reducing the competition for assimilates between spike and culm is of particular importance in wheat cultivar improvement. The dramatic improvement in wheat yield throughout the world in the second half of the 20th century is thought to be associated with improved partitioning of assimilates to the spike caused by introducing semi-dwarf genes (Slafer et al., 1994). Thus, plant growth retardants may be utilized to simulate the effect of reducing plant height on crop growth.

Chlormequat, an anti-gibberellin, is often applied to shorten the lengths of stem, culm and internodes of wheat, potato and hibiscus in Japan (NARO, 2006). Although the primary aim of chlormequat application is preventing lodging, an increase in grain yield of wheat has been reported in Japan (Fukushima et al., 1990; Wada et al., 1991). Ecophysiological causes of the yield increase in wheat induced by chlormequat application have been studied in the UK (Craufurd and Cartwright, 1989; Olumekun, 1996), but not yet in Japan. On the other

Received 2 February 2009. Accepted 22 May 2009. Corresponding author: M. Toyota (toyota@ag.kagawa-u.ac.jp, fax +81-87-891-3058). **Abbreviations**: AGDM, aboveground dry matter; DAS, days after sowing; HI, harvest index; K, extinction coefficient in canopy; LAI, leaf area index; MTA, mean tip angle of the canopy; PAR, photosynthetically active radiation; RUE, radiation-use efficiency; Si, cumulative total solar radiation intercepted by the plant canopy. hand, excess shortening of plant height should lower the ability of the canopy to produce biomass by deteriorating leaf geometrical attributes. To evaluate the effect of changing plant height on crop growth, it is essential to know the light interception characteristics and the radiation-use efficiency (RUE) of the canopy (Monteith, 1977; Gallagher and Biscoe, 1978). However, there is very limited information on the effects of chlormequat-induced culm length reduction on crop growth, light interception characteristics and RUE in Japan.

This study aimed to clarify the light interception characteristics and RUE in the leading wheat cultivar of Kagawa Prefecture in southwest Japan as well as the effects of reducing plant height induced by chlormequat on these traits.

Materials and Methods

1. Site and crop management

A field experiment was conducted in the experimental field of the Faculty of Agriculture, Kagawa University (N34°16'17", E134°7'39"), from the autumn of 2006 to the spring of 2007. A spring-type wheat cultivar, Sanukinoyume 2000, which was developed by the Kagawa Prefecture Agricultural Experiment Station, was used in this study. The plants were grown in 6 plots of 7.2 m length $\times 1.2$ m in the east-to-west direction 0.8 m apart. Each plot consisted of 36 rows of 1.2 m length in the north-to-south direction with a row distance of 0.2 m. On 14 November, 2006, 40 seeds per row were hand-sown to establish wheat stands with a plant density of approximately 150 plants m². Plots were fertilized the day before sowing with 60 kg ha⁻¹ of N, P₂O₅ and K₂O using a compound fertilizer. Supplemental nitrogen, 20 kg ha⁻¹ of N, was applied in the form of ammonium sulfate on 10 February, 2007 (88 d after sowing, DAS). Pendimethalin (Go-Go-San, BASF Agro, Co., Ltd.) was sprayed on the soil surface after sowing to control weeds.

2. Treatment

Chlormequat chloride (Cycocel, Sankyo, Co., Ltd.) at a 0.2% concentration was sprayed on the plant canopy at the beginning of jointing (27 February, 2007, 105 DAS). Three alternated replicate plots were prepared for control and chlormequat treatments.

3. Measurements

Aboveground dry matter (AGDM) was measured 7 times for the sample collected from 0.3 m (64 and 91 DAS), 0.6 m (105 and 119 DAS) and 1.2 m (133, 147 and 161 DAS) of each row of stands. A section, which consisted of 6 consecutive uniform rows of stands, was selected in each plot for measurements of solar radiation, leaf area index (LAI) and yield. The total solar radiation intercepted by the plant canopy was determined by constant measurements of total solar radiation above the canopy with a dome pyranometer (CM3, Campbell Scientific, Inc.) and below the canopy with 0.97 m long tube solarimeters (TSL-05, Delta-T Devices, Ltd.). The dome pyranometer was placed 1.5 m above the soil surface at the center of the experimental field. Two tube solarimeters for each treatment were installed at two different replicate plots. All tube solarimeters were placed at the center of the section of each plot along the row at ground level. Radiation measurement at the experimental field was performed from 16 January (63 DAS). Nondestructive measurement of LAI and mean tip angle of the canopy (MTA) using a plant canopy analyzer (LAI-2000, Li-Cor, Inc.) (Welles and Norman, 1991) was performed weekly from 17 January (64 DAS) to 24 April (161 DAS) in the same section where the intercepted radiation and yield were measured.

Extinction coefficient of canopy(K) was estimated from the following formula:

 $K = -ln (I / I_0) / L$

where, I_0 is the incident solar radiation above the canopy and I is the amount of solar radiation below the canopy which has an LAI value of L (Monsi and Saeki, 1953.

Radiation-use efficiency (RUE, g MJ⁻¹) was estimated from the slope of the linear regression of cumulative total solar radiation intercepted by the plant canopy (Si) vs AGDM from the start of sampling (17 January, 64 DAS) to the sampling nearest to heading (10 April, 147 DAS) and to the sampling nearest to anthesis (24 April, 161 DAS). RUE values in this study are based on total solar radiation. A reference RUE value, which is based on photosynthetically active radiation (PAR), is converted to total solar radiation by multiplying by 0.5 (Sinclair and Muchow, 1999).

Air temperature 1.5 m aboveground level, total solar radiation and rainfall measured at the weather station located adjacent to the experimental field were also used as a reference.

At maturity, the aboveground biomass of a section (1.44 m^2) in each plot was sampled. AGDM, grain yield, 1000-grain weight and the number of spikes were recorded after the samples were dried for 4 wk in a glasshouse. The numbers of grains per unit area and the grains per spike were estimated from the grain yield, 1000-grain weight and the number of spikes per unit area. The harvest index (HI) was calculated as the ratio of grain yield to AGDM. In addition, 15 main shoots per plot were randomly sampled at anthesis and maturity, and the lengths of spike and culm were recorded.

Results

1. Phenology and weather conditions

Seedling emergence started about 10 d after sowing, and the jointing stage started about the end of February. The dates of heading and anthesis in the control plants



Fig. 1. Mean air temperature (a), mean of daily solar radiation (b) and cumulative precipitation (c) at the experimental site in 10 successive days from November 2006 to May 2007 (closed circles and bars). Open circles represent the mean of 9 years from 1997 to 2005.

Table 1. Effects of chlormequat application on the lengths of spike, culm and spike plus culm of the main culm at anthesis and maturity in wheat.

Plat	Spike	Culm	Spike+Culm		
Flot	(cm)	(cm)	(cm)		
Control	8.8	89.7	98.5		
Chlormequat	8.4	78.4	86.8		
t-test	***	***	***		

*** Significant at P<0.001.

were 2 April (139 DAS) and 18 April (155 DAS), respectively, whereas those in chlormequat-treated plants were 4 April (141 DAS) and 19 April (156 DAS), respectively. The control plants and chlormequat-treated plants reached maturity on 29 May (196 DAS). Thus, chlormequat treatment delayed heading by 2 d and anthesis by 1 d compared with the control. Weather data at the weather station during the experimental period is summarized in Fig. 1. Mean air temperature at sowing was 12.1°C. It decreased to 5.5°C in the middle of January, and then increased to 11.5, 13.0 and 20.0°C at heading, anthesis and maturity, respectively. Mean of daily solar radiation at



Fig. 2. Change of aboveground dry matter (AGDM) (a), LAI (b) and cumulative total solar radiation intercepted by the wheat canopy (Si) (c). Vertical bars indicate the standard error of the mean. Arrow indicates the time of chlormequat application. The time of heading and that of anthesis in the controls are indicated by open triangles, and those in the chlormequattreated plants by closed triangles.

sowing, heading, anthesis and maturity was 8.6, 19.8, 20.0 and 26.2 MJ m⁻² d⁻¹, respectively. The minimum of daily solar radiation (6.3 MJ m⁻² d⁻¹) was recorded in the first ten days of December. Cumulative daily solar radiation from sowing to maturity was 2917 MJ m⁻². Total rainfall during the experimental period was 199 mm. No symptoms of water stress were observed in the plants.

2. Plant height

Table 1 shows the spike length and culm length of the main stem sampled at anthesis and maturity. Chlormequat application significantly shortened the spike, culm and spike plus culm length by 4.5%, 12.6% and 11.9%, respectively, compared with the controls. Lodging did not occur in either the control or chlormequat-treated plants until harvest.

Table 2. Effects of chlormequat application on aboveground dry matter (AGDM), LAI, extinction coefficient in canopy (K), cumulative total solar radiation intercepted by wheat canopy (Si) and radiation use efficiency (RUE). AGDM, LAI and K values were obtained from samples taken at heading (H) and anthesis (A). Si and RUE were the values from the first sampling to heading (F-H) and to anthesis (F-A).

Plot	AGDM	(g m ⁻²)	LAI		К		Si (MJ m ⁻²)		RUE (RUE $(g M f^1)$	
	Н	А	Н	А	Н	А	F-H	F-A	F-H	F-A	
Control	1197	1509	5.9	5.9	0.42	0.47	776	968	1.44	1.55	
Chlormequat	1011	1527	5.5	5.6	0.43	0.48	721	909	1.34	1.57	
t-test	ns	ns	ns	ns	ns	ns	ns	ns	-	_	

ns, Not significant at P<0.05; -, t-test was not performed.



Fig. 3. Extinction coefficient (K) in wheat canopy. Vertical bars indicate the standard error of means. Arrow indicates the time of chlormequat application. The time of heading and that of anthesis in the controls are indicated by open triangles, and those in the chlormequat-treated plants by closed triangles.

3. Crop growth

Fig. 2 shows AGDM, LAI and Si from the first sampling day to anthesis. AGDM, LAI, and K values at heading and anthesis, and Si and RUE values from the first sampling to heading and from the first to anthesis sampling are summarized in Table 2. AGDM of chlormequat-treated plants at the first sampling was about 35 g m⁻², and it increased to 1011 and 1527 g m^2 at heading and anthesis, respectively. Chlormequat had no significant effect on AGDM at any sampling time (Fig. 2, Table 2). LAI increased from about 0.3 at the first sampling to 5.5 at heading and 5.6 at anthesis in chlormequat-treated plants. Si of chlormequat-treated plants at heading was 7.1% and at anthesis was 6.1% smaller than control values. LAI and Si of chlormequat-treated plants were consistently lower than those of controls but there were no significant differences between treatments at any date for both these traits (Fig. 2, Table 2).

4. Radiation interception, RUE and MTA

Fig. 3 illustrates the changes in extinction coefficient in canopy(K). In both chlormequat-treated and control plants, the mean K increased from 0.4 at 64 DAS to 0.5 at 90 DAS, then decreased to 0.37 a week before heading



Fig. 4. Relationship between cumulative aboveground dry matter (AGDM) and cumulative total solar radiation intercepted by the wheat canopy (Si) from the first sampling day (64 DAS) to anthesis (161 DAS). Fitted lines are estimated by the following linear regressions. Control: y=1.554 x-71.3 (r=0.986, P<0.001); Chlormequat: y=1.565 x-35.5 (r=0.986, P<0.001).</p>

(133 DAS). Thereafter, it rose to about 0.5 at anthesis (Table 2). The standard error of K was large at the beginning, but it gradually decreased as time elapsed. The mean K during the entire period was the same (0.46) in both chlormequat-treated and control plants.

There was a close linear relationship between Si and AGDM in both treated and control plants (Fig. 4). The RUE estimated from the slope of the linear regression of Si vs AGDM was nearly the same in both treated and control plants. The RUE from the first sampling to heading was 1.44 and 1.34 g MJ m² in the control and chlormequat-treated plants, respectively, and the RUE from the first sampling to the anthesis was 1.55 and 1.57 g MJ m² in control and chlormequat-treated plants, respectively (Table 2).

MTA in controls was 75° at the first sampling day, decreased to 59° at 91 DAS, and again increased to 63° at 98 DAS, then gradually decreased to 46° at anthesis (Fig. 5). The change of MTA with time in the chlormequat-treated plants was basically the same as that in the controls, but MTA at anthesis was significantly higher in the chlormequat-treated plants than in the controls.

5. Yield

Table 3 summarizes the yield, yield components and HI

value at maturity (5 May, 196 DAS). Because very uniform wheat stands were established and there were no particular constraints during plant growth, grain yields were high for both control and chlormequat-treated plants, 863 and 911 g m⁻², respectively. Although almost all traits of chlormequat-treated plants except 1000-grain weight and AGDM were higher than those of controls, the difference was significant only for HI, which was 41.1% in the chlormequat-treated plants and 38.7% in the control plants.

Discussion

Chlormequat application shortened the culm length by 12.6% relative to controls (Table 1), but did not affect AGDM, yield or yield components except for HI (Fig. 2, Tables 2 and 3). The high HI in chlormequat-treated plants could be attributable to a higher partitioning ratio of assimilate to spike due to reducing culm length. However, Craufurd and Cartwright (1989) reported that the effect of chlormequat was similar to that of short days: flowering was delayed and tiller production increased. Thus, there is a possibility that a higher HI in chlormequat-treated plants was attributed to the slow plant development, which may increase productive tillers and survival rate of florets. This



Fig. 5. Time course of mean tip angle (MTA) of the wheat canopy. Vertical bars indicate the standard error of the mean. Arrow indicates the time of chlormequat application. The time of heading and that of anthesis in the controls are indicated by open triangles, and those in chlormequat treated-plants by closed triangles.

* Significant at P<0.05.

speculation is supported by the results of the present study, because chlormequat delayed the heading and anthesis time by two and one day, respectively, compared to the controls. Nevertheless, the results of the present study provide useful information on the effect of reducing plant height on crop growth, particularly in radiation interception and RUE.

According to the review by Sinclair and Muchow (1999), the RUE values in wheat ranged from 0.73 to 1.62 g M_{1}^{-1} , and they considered that the value of 1.46 g MJ⁻¹ estimated by Yunusa et al. (1993) reflects the potential RUE. In Japan, Takahashi and Nakaseko (1990) showed that RUE of spring wheat increased from about 3g MI⁻¹ at the double ridge stage to 5 g MJ⁻¹ at flag leaf emergence. (These RUE values are based on PAR, and are equivalent to 1.5 and 2.5 g MJ⁻¹ based on total radiation.) Kamoshita (2002) reported RUE values of 0.98 g M⁻¹ in sparse planting and 1.07 g MJ⁻¹ for dense planting of winter wheat. On the other hand, Green (1986) commented that information on the influence of chlormequat on RUE is limited, and today, the situation is the same. In the present study, the RUE value estimated based on data from the first sampling day to anthesis was 1.55 g M^{-1} in controls, and was not affected by chlormequat application (Table 2). This RUE value is higher than previously reported values, but the RUE values estimated based on the data from the first sampling to heading, i.e. 1.44 in the control and 1.34 g M⁻¹ in the chlormequat treatment (Table 2), were not as high as those estimated based on the data up to anthesis.

Reduction of LAI by chlormequat application in wheat and barley have been reported (Robertson and Greenway, 1973; Bragg et al., 1984; Green at al., 1985). In the present study, although there were no significant differences between chlormequat-treated and control plants at any sampling date, the LAI values in the chlormequat-treated plants were always lower than those in the control (Fig. 2, Table 2). Information on the effect of chlormequat on light interception in the wheat canopy is limited, but in barley, Green et al. (1985) reported on the chlormequatinduced increase in K. In the present study, there was no clear difference in the time course of K between the treatments and the mean values of K for all dates of sampling were the same (0.46) (Fig. 3). Thus, the LAI and K values were not significantly affected by chlormequat

Table 3. Effects of chlormequat application on grain yield, yield components, aboveground dry matter (AGDM) and harvest index (HI) at harvest in wheat.

Plot	Grain yield (g m ⁻²)	Grain no. (m²)	1000 grain weight (g)	Spike no. (m²)	Grain no. per spike	AGDM (g m ⁻²)	HI (%)
Control	863 ± 23.5	23239 ± 1117	37.2 ± 0.8	763 ± 18	30.4 ± 0.8	2231 ± 40.6	38.7 ± 0.4
Chlormequat	911 ± 6.4	24796 ± 260	36.8 ± 0.2	$770\!\pm\!29$	32.3 ± 0.9	2218 ± 53.2	41.1 ± 0.7
t-test	ns	ns	ns	ns	ns	ns	*

Means±S.E. * Significant at P<0.05; ns, not significant at P<0.05.



Fig. 6. Relationship between relative radiation intensity penetrating to the ground level (I/I₀) and leaf area index (LAI) in wheat. Fitted lines are estimated by the following exponential regressions. Control: I/I₀=0.0450+0.9587 exp (-LAI/1.8814) (R^2 =0.995); Chlormequat: I/I₀=0.0582+0.9824 exp (-LAI/1.9565) (R^2 =0.994).

application, so that Si was also not significantly affected (Fig. 2). This result, however, should be natural because the LAI at the time when the treatment (DAS 105) was as large (2.96 in the control and 2.77 in the chlormequattreated plants), which intercepted almost all incident solar radiation. Accordingly, the relative radiation intensity penetrating to the ground level (I / I_0) at that time was 0.24 in the control and 0.30 in the chlormequat-treated plants (Fig. 6). A week later (DAS 112), I/I_0 was decreased further to 0.17 in the control and 0.21 in the chlormequattreated plants with increasing LAI (i. e. 4.39 in the control and 3.88 in the chlormequat-treated plants). These results suggested that the amount of intercepted radiation was high enough at the beginning of this experiment, which resulted in no significant difference in Si between the control and chlormequat treatment.

Although data was not presented, Wada et al. (1991) reported improvement of light interception by chlormequat application due to short, erect leaves. This observation is supported by the significantly higher MTA in chlormequat-treated plants at anthesis (Fig. 5). In spite of the Si in chlormequat was not significantly different from that of the control, a higher MTA in chlormequat should provide effective distribution of radiation within the canopy, which should increase a photosynthetic performance (Angus et al., 1972; Innes and Blackwell, 1983; Green et al., 1985). Even if that was the case, however, the effect of higher MTA in chlormequat on photosynthetic performance should be restricted to the duration from about the heading time to the premature ripening stage (Fig. 5).

In conclusion, chlormequat application in wheat cultivar Sanukinoyume 2000, produced in Kagawa Prefecture of southwest Japan, significantly shortened the plant height. However, chlormequat application didn't significantly affect AGDM, yield or yield components except for HI (Tables 1 and 3; Fig. 2). The traits related to light interception, namely, LAI and K, were not affected by chlormequat treatment either (Figs. 2, 3), which resulted in the same amount of Si (Fig. 2). Although MTA of chlormequat was significantly higher than those of control at anthesis (Fig. 5), it didn't significantly affect Si. RUE was also not affected by chlormequat application (Fig. 4). These results suggest that shortening the culm length of the current leading wheat cultivar by about 12% is beneficial in reducing the risk of lodging without affecting the light interception characteristics or RUE.

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* In Japanese with English title.

** In Japanese. The present authors translated the title from Japanese.