Effect of drought on ear and flag leaf photosynthesis of two wheat cultivars differing in drought resistance

T. INOUE*, S. INANAGA*, Y. SUGIMOTO**, P. AN*, and A.E. ENEJI*

*Arid Land Research Center, Tottori University, 1390 Hamasaka, Tottori 680-0001, Japan**
Department of Biofunctional Chemistry, Faculty of Agriculture, Kobe University,
*1-1 Rokkodai-cho, Nada-ku, Kobe 657-8501, Japan***

Abstract

We investigated net photosynthetic rate (P_N) of ear and two uppermost (flag and penultimate) leaves of wheat cultivars Hongmangmai (drought resistant) and Haruhikari (drought sensitive) during post-anthesis under irrigated and non-irrigated field conditions. The P_N of ear and flag leaf were significantly higher and less affected by drought in Hongmangmai than in Haruhikari. The rate of reduction in stomatal conductance (g_s) was similar for the two cultivars, but intercellular CO_2 concentration (C_i) in the flag leaf of Hongmangmai was lower than that of Haruhikari in non-irrigated treatment. No differences were observed in leaf water potential (ψ_l) and osmotic adjustment of the flag leaf of the cultivars. These results imply that differences in photosynthetic inhibition on the flag leaf at low leaf ψ_l between the cultivars were primarily due to non-stomatal effects. Hence the main physiological factor associated with yield stability of Hongmangmai under drought stress may be attributed to the capacity for chloroplast activity in the flag leaf, which apparently allows sustained P_N of flag leaf during grain filling under drought stress. The higher P_N of ear in Hongmangmai under drought could also be related to its drought resistance.

Additional key words: cultivar differences; diurnal change; intercellular CO_2 concentration; net photosynthetic rate; stomatal conductance; *Triticum aestivum*; water stress.

Introduction

Grain growth in wheat depends on carbon from three sources: current assimilation, remobilization of pre-anthesis assimilates stored in the stem and other plant parts, and re-translocation of assimilates stored temporarily in the stem after anthesis (Kobata *et al.* 1992). Post-anthesis drought reduces carbon assimilation and hence the availability of current assimilates for grain filling, but probably does not affect the translocation of carbon to the grain (Wardlaw 1967, Johnson and Moss 1976).

Approximately 70 to 90 % of the final grain yield is derived from photosynthates made during the grain filling periods under favourable conditions (Austin *et al.* 1977, Bidinger *et al.* 1977). Most of the assimilates used for grain growth is produced by the upper canopy, which derives mainly from the spike, the flag leaf, and its sheath (Evans *et al.* 1972, Austin *et al.* 1977, Makunga *et al.* 1978, Morgan and Austin 1983, Loss and Siddique 1994). The photosynthetic activity of flag leaves is especially important during grain filling when the older leaves begin senescing (Loss and Siddiqeu 1994, Turner 1997).

Several researchers suggested that the ear assumes a greater role than flag leaves in supplying assimilates to the grain when drought stress develops (Evans *et al.* 1972, Johnson and Moss 1976, Blum 1985). Photosynthetic contribution of ear and the two uppermost leaves to grain mass per ear was different between genotypes (Wang *et al.* 2001). However, most studies on responses of photosynthetic organs to drought stress have been performed only on leaves. Furthermore, cultivar responses in ear photosynthesis to drought stress have not been examined.

The effects of drought on leaf photosynthesis are well documented (*e.g.* Kaiser 1987, Chaves 1991). Sharkey and Seemann (1989) concluded that reductions in whole leaf photosynthesis caused by mild drought stress are primarily the results of stomatal closure and that there is no indication of damage to chloroplast reactions. At more severe drought stress, photosynthesis continues to decrease, while the ratio of intercellular/ambient CO_2 concentration increases significantly to values similar to those obtained in well watered plants (Rekika *et al.* 1998). Thus, the decrease in photosynthesis could result

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E-mail: sapana1975@hotmail.com
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from non-stomatal factors affecting photosynthetic capacity, *e.g.* reduced activity of some Calvin cycle enzymes, inhibition of photosynthetic electron transport, and impaired photophosphorylation capacity (Sharkey and Seemann 1989, Kicheva *et al.* 1994). There exist genotypic variations in the effect of drought stress on stomatal conductance (g_s) and net photosynthetic rate (P_N) (Johnson *et al.* 1987, Matin *et al.* 1989).

A better understanding of the mechanisms that enable wheat plants to adapt to drought stress and maintain growth, development, and productivity during stress periods would help in breeding for drought resistance (Seropian and Planchon 1984). Hongmangmai is a popular local cultivar in the Loess Plateau, China (Inanaga 1989), and is known to be drought resistant. Our recent work on this cultivar showed that maintenance of post-anthesis photosynthesis was related to drought resistance rather than remobilization of pre-anthesis assimilates to grain under drought stress (Inoue *et al.* 2004). However, the specific mechanisms mediating the resistance to drought stress in Hongmangmai were not identified. In this study, post-anthesis photosynthesis and leaf water relations were compared between this drought resistant wheat cultivar and a drought sensitive cultivar (Haruhikari) to determine if these physiological parameters contribute to drought resistance in Hongmangmai.

Materials and methods

The field experiment was conducted at the Arid Land Research Center, Tottori University, Japan (35°32'N, 134°13'E) from November 1997 to June 1998. The field was covered with transparent plastic sheets which permitted transmission of more than 95 % of incident solar radiation. The soil at the experimental site was sandy with about 98 % sand (Ikeura *et al.* 1998). The experimental design was a split-plot with three replications. The main plots consisted of irrigated and non-irrigated treatments. The sub-plots consisted of two tall wheat (*Triticum aestivum* L.) cultivars: Hongmangmai, a drought resistant local cultivar grown in the Loess Plateau, China and Haruhikari, a Japanese drought sensitive cultivar with high yielding potential under favourable conditions. Subplots were separated by plastic plates, vertically buried to a depth of 60 cm.

Seeds were sown on 20 November 1997 into plots with seven rows 189 cm long. Inter-row spacing was 35 cm and interplant spacing was 9 cm. A compound fertilizer (N-P_2O_5-K_2O, 13-15-15) was applied before planting at the rate of 60 g m^{-2}. Water was applied at the rate of 0.1 m^3 m^{-2} every few days to maintain the soil water content close to field capacity. On 2 January 1998, drought stress treatment was initiated by withholding water from non-irrigated plots until maturity. Irrigation was continued in the irrigated plots during the growing period to maintain the soil water potential near field capacity.

Measurements of gas exchange rate and leaf water status were made near midday (10:00–14:00) on 29 March (86 d after treatment, DAT), 10 April (98 DAT), 5 May (123 DAT), 6 May (124 DAT), 14 May (132 DAT), 22 May (140 DAT), and 1 June (150 DAT). The P_N, g_s, and C_i were measured with a portable photosynthesis system *LI-6400* (*LI-COR*, Lincoln, USA) on the uppermost fully expanded leaves and the penultimate leaves of randomly selected plants. Photosynthetically active radiation (PAR) of 1 800 μmol m^{-2} s^{-1} was provided at each measurement by *6400-02* Light Source. The gas exchange rate of the ear was measured with a portable photosynthesis system *LI-6200* (*LI-COR*, Lincoln, USA) with the *6000-13* Quarter Liter Chamber. At 123 DAT, flag leaf P_N was measured throughout the day. At each set of the diurnal measurement, irradiation was set for the actual reading of the external quantum sensor. Leaf area of flag and penultimate leaves was measured using a *LI-COR* Portable Area Meter (*LI-3000*). The ear surface area was calculated by the assumption that ear surface area = length×width×3.8 (Qui and Zhai 1985). Leaf water status was measured near midday on 5 May (123 DAT). A pressure chamber (model *1000*, *PMS*, Oregon, USA) was used for leaf water potential (ψ_l) measurements and relative water content was determined as described by Kobata (1984). After ψ_l measurements, the samples were wrapped in aluminum foil, immediately frozen in liquid nitrogen, and stored at –20 °C (Rekika *et al.* 1998). The osmotic potential of the sap of these samples was measured by a freezing point osmometer (*OM 801*, *Vogel, Medizinische Technik und Elektronik*, Berlin, Germany). Osmotic adjustment was estimated according to Wright *et al.* (1983).

Aboveground dry matter (DM) was taken on 11 April (99 DAT) and at physiological maturity. Irrespective of treatment, the flag leaf of the two cultivars was already fully expanded 99 DAT. Leaf area was measured 99 DAT using an automatic area meter (*AAC-410, Hayashi Denko Co.*, Tokyo, Japan) to estimate leaf area index (LAI). At each harvest, 16 plants were sampled, oven-dried at 80 °C, and weighed. The ears were then threshed by hand, and grain mass recorded. Analysis of variance and *t*-test were used to analyze the experimental data.

Results

Cultivar effects were highly significant for grain yield and total shoot DM at maturity (p<0.001), and significant for total shoot DM at 99 DAT (p<0.05) (Table 1). There were highly significant (p<0.001) irrigation effects for all parameters measured, except for total shoot DM at 99 DAT which was significant (p<0.01). The cultivar× irrigation interaction was either highly significant or significant for all the parameters, except for LAI at 99 DAT. Irrigation effects for grain yield and total shoot DM at 99 DAT and maturity differed according to the cultivars. Grain yield and total shoot DM of Hongmangmai were reduced less by drought than those of Haruhikari. The difference in total shoot DM between 99 DAT and maturity was lower in non-irrigated Haruhikari than in Hongmangmai.

The effect of drought stress on P_N of ear was different between the cultivars (Fig. 1*C*). Under non-irrigated treatment, Hongmangmai showed higher P_N of the ear than Haruhikari. The P_N of flag leaf in both cultivars was higher under irrigated treatment than in the non-irrigated treatment (Fig. 1*B*). Hongmangmai maintained higher P_N than Haruhikari in the non-irrigated treatment. Under irrigated treatment, the P_N of the flag leaf of the two cultivars decreased after anthesis, then increased at 132 DAT, and decreased again thereafter. Flag leaf P_N in non-irrigated treatment decreased in Hongmangmai prior to anthesis; it increased after anthesis and then declined. Non-irrigation gradually decreased the P_N of flag leaf in Haruhikari as drought stress increased. The P_N of penultimate leaf in both cultivars declined gradually under non-irrigated treatment, but the difference between the treatments in Hongmangmai was less than in Haruhikari (Fig. 1*A*).

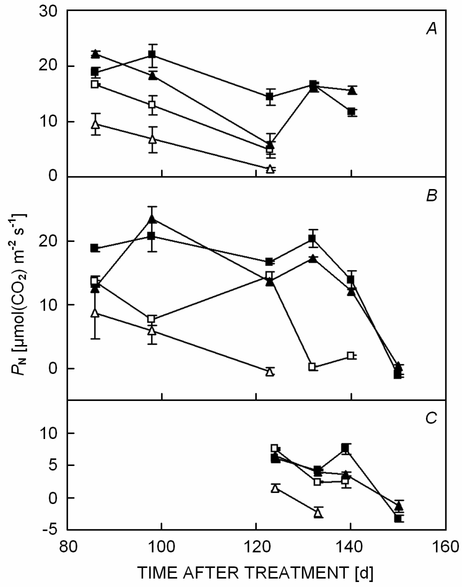

Fig. 1. Net photosynthetic rate (P_N) of penultimate leaf (*A*), flag leaf (*B*), and ear (*C*) of two wheat cultivars grown in irrigated and non-irrigated treatments. ■ Hongmangmai, irrigated; □ Hongmangmai, non-irrigated; ▲Haruhikari, irrigated; Δ Haruhikari, non-irrigated. *Bars* indicate ± SE of the mean where values exceed the size of the symbol.

Table 1. Grain yield [g m^{-2}], total shoot dry matter (DM) [g m^{-2}] at 99 DAT and maturity, and leaf area index (LAI) at 99 DAT of two wheat cultivars grown in irrigated and non-irrigated treatments. NS, *, **, ***; not significant, significant at 5, 1, and 0.1 %, respectively, according to analysis of variance.

Cultivar	Treatment	Grain yield	Total shoot DM		LAI
			99 DAT	Maturity	99 DAT
Hongmangmai	Irrigated	286	436	844	3.4
	Non-irrigated	150	389	453	2.0
Haruhikari	Irrigated	436	589	1158	3.5
	Non-irrigated	106	392	363	1.4
Variation source	Cultivar	***	*	***	NS
	Treatment	***	**	***	***
	Interaction	***	*	***	NS

In the irrigated treatment, P_N of flag leaf of the two cultivars increased until 12:00, then decreased (Fig. 2). Non-irrigated Hongmangmai also attained maximum P_N at midday, while Haruhikari reached the maximum at 06:00. Hongmangmai maintained higher P_N during the daytime than Haruhikari under non-irrigated treatment.

The P_N of ear in non-irrigated Hongmangmai was not affected at midday 124 DAT, while that of Haruhikari decreased by 76 % under non-irrigated treatment (Table 2). There were significant (p<0.05) reductions in g_s and C_i for both cultivars under the non-irrigated treatment, but interaction effects were not significant for these parameters.

Flag leaf P_N of Hongmangmai was only slightly reduced under non-irrigated condition, while that of Haruhikari was greatly decreased in non-irrigated treatment (Table 2). The effect of non-irrigation on g_s was similar for both cultivars. The C_i in Hongmangmai was similar in both treatments, but that of Haruhikari was increased by 151 % under non-irrigated treatment.

P_N of penultimate leaves in both cultivars showed similar reductions under non-irrigated conditions (Table 2). Drought stress decreased g_s in Hongmangmai, but not in Haruhikari. There were no significant differences in C_i between treatments in Hongmangmai, while non-irrigated treatment increased it by 445 % in Haruhikari.

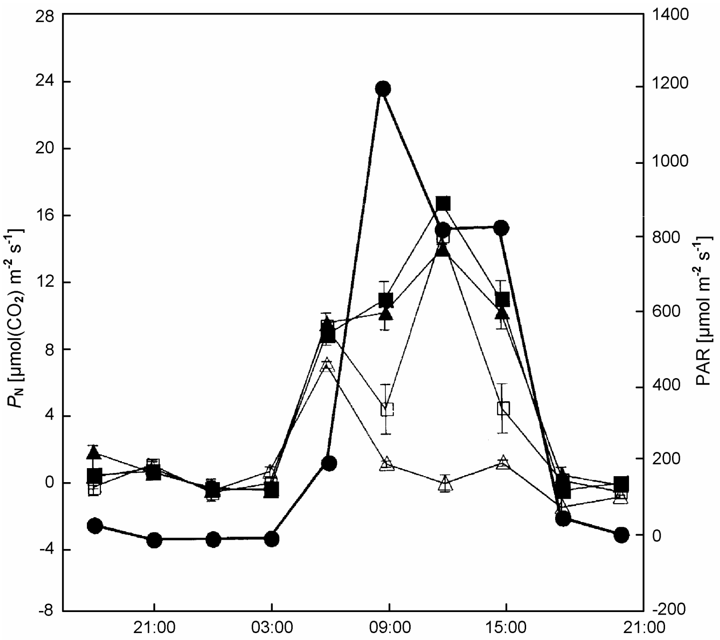

Fig. 2. Diurnal changes in net photosynthetic rate (P_N) of flag leaf of two wheat cultivars grown in irrigated and non-irrigated treatments at 123 DAT. ■ Hongmangmai, irrigated; □ Hongmangmai, non-irrigated; ▲Haruhikari, irrigated; Δ Haruhikari, non-irrigated; ● photosynthetically active radiation (PAR). *Bars* indicate ± SE of the mean where values exceed the size of the symbol.

There were highly significant irrigation effects on flag and penultimate leaf area ($p<0.001$), and significant treatment effect for ear surface area ($p<0.01$) (Table 3). Cultivar effect was either highly significant or significant for the flag and penultimate leaf area. The cultivar×treatment interaction was only highly significant for flag leaf area ($p<0.001$). Flag leaf area showed similar values for the two cultivars in the irrigated treatment, but non-irrigation reduced the flag leaf area of only Hongmangmai.

Significant treatment and cultivar effects were noted for flag leaf ψ_l at midday (Table 3). The effect of irrigation on flag leaf ψ_l was similar for both cultivars. Non-irrigated treatment reduced the ψ_l of the penultimate leaf in Hongmangmai but not in Haruhikari. There were no significant differences in osmotic adjustment of both cultivars, irrespective of the leaf positions (Table 3).

Discussion

The drought resistant cultivar Hongmangmai had a higher grain yield than Haruhikari under drought, and the reduction in grain yield under drought was smaller in Hongmangmai than in Haruhikari (Table 1). This apparent drought resistance of Hongmangmai was associated with the dry matter accumulation during grain filling, resulting from the continued increase in total shoot DM between 99 DAT (after flag leaf expanded) and maturity. On the contrary, the drought sensitive Haruhikari did not show any increase in total shoot DM between 99 DAT and maturity under drought, leading to a lower grain yield. When assimilates available from post-anthesis photosynthesis satisfy the requirements for grain filling in wheat, a high grain yield may be achieved (Flood *et al.* 1995, Ehdaie and Waines 1996).

Both the flag leaves and the inflorescence have a major role in determining wheat grain yield (Shimshi and Ephrat 1975). Under drought stress, the P_N of flag leaf and ear were significantly higher in Hongmangmai than in Haruhikari during grain filling (Fig. 1). However, the decrease in P_N of the penultimate leaf during post-anthesis was similar in the two cultivars. The extent of depression in P_N by drought was similar among plant parts and close to zero in Haruhikari, but varied among plant parts in Hongmangmai. Xu *et al.* (1987) also reported that the depression in photosynthesis by drought was larger in the lower leaves than in the upper ones and the depression was smaller in the ear than in the leaves. Similar result was obtained for barley (Sánchez-Díaz *et al.* 2002). In contrast to potted plants (Johnson *et al.* 1974), under a more gradual and prolonged conditions of stress as it occurred in the field (Evans *et al.* 1972, Johnson and

Moss 1976), the spikes were less adversely affected by drought than were leaves. The ear P_N of Hongmangmai was unaffected by irrigation, but the flag leaf P_N was slightly inhibited by drought stress. Therefore, from the results obtained in this research, we may conclude that ear and flag leaf P_N of Hongmangmai were less affected by drought than that of Haruhikari, and this induced higher grain yield in Hongmangmai under drought.

Table 2. Influence of irrigation treatment on net photosynthetic rate (P_N) [μmol(CO_2) m^{-2} s^{-1}], stomatal conductance (g_s) [mol(H_2O) m^{-2} s^{-1}], and intercellular CO_2 concentration (C_i) [μmol(CO_2) m^{-2}] of ear (124 DAT), and flag and penultimate leaves (123 DAT) of two wheat cultivars. NS, *, **, ***; not significant, significant at 5, 1, and 0.1 % level, respectively, according to analysis of variance.

	Cultivar	Treatment	P_N	g_s	C_i
Ear	Hongmangmai	Irrigated	6.0	0.11	278
		Non-irrigated	7.5	0.08	175
	Haruhikari	Irrigated	6.5	0.11	329
		Non-irrigated	1.5	0.07	300
	Variation source	Cultivar	**	NS	**
		Treatment	*	*	*
		Interaction	***	NS	NS
Flag leaf	Hongmangmai	Irrigated	16.6	0.34	266
		Non-irrigated	14.6	0.19	226
	Haruhikari	Irrigated	13.8	0.21	242
		Non-irrigated	–0.3	0.03	365
	Variation source	Cultivar	***	***	**
		Treatment	***	***	*
		Interaction	***	NS	***
Penultimate leaf	Hongmangmai	Irrigated	14.4	0.17	201
		Non-irrigated	5.0	0.05	198
	Haruhikari	Irrigated	6.0	0.03	60
		Non-irrigated	1.5	0.05	266
	Variation source	Cultivar	**	**	NS
		Treatment	**	*	**
		Interaction	NS	*	**

Table 3. Influence of irrigation treatment of two wheat cultivars on the areas [cm^2] of ear, flag, and penultimate leaves at 123 and 124 DAT and on xylem water potential (ψ_l) and osmotic adjustment (OA) [MPa] of flag and penultimate leaves at 123 DAT. NS, *, **, ***; not significant, significant at 5, 1, and 0.1 % levels, respectively, according to analysis of variance.

Cultivar	Treatment	Area			ψ_l		OA	
		Flag leaf	Penult. leaf	Ear	Flag leaf	Penult. leaf	Flag leaf	Penult. leaf
Hongmangmai	Irrigated	27	43	52	–2.0	–2.0	0.13	1.11
	Non-irrigated	15	30	26	–2.8	–2.5		
Haruhikari	Irrigated	28	33	56	–2.3	–2.0	0.18	0.40
	Non-irrigated	26	24	41	–3.0	–2.1		
Variation source	Cultivar	***	**	NS	**	NS	NS	NS
	Treatment	***	***	**	***	*		
	Interaction	***	NS	NS	NS	*		

Photosynthetic capacity is determined by total leaf area as well as photosynthesis per unit surface area. Simpson (1968) reported that the area above the flag leaf internode was positively and highly correlated with grain yield of 120 cultivars of wheat. Under drought stress, the flag leaves in less irrigated treatment were shorter and narrower than those of normal irrigated wheat (Zhang *et al.* 1998). The area of ear and the penultimate leaf showed a similar reduction with both cultivars under non-irrigated treatment, while the flag leaf area of Hongmangmai was more reduced than that of Haruhikari under drought (Table 3). Hongmangmai maintained a higher photosynthetic rate of ear, although the area of ear was similar in both cultivars, suggesting a more efficient photosynthesis per ear. While the area of flag leaf in Hongmangmai was reduced more than in Haruhikari, Hongmangmai also maintained a higher photosynthetic rate in the flag leaf even under drought when P_N in

Haruhikari was close to zero. This suggested that Hongmangmai also had a higher photosynthetic rate per flag leaf than Haruhikari.

In Haruhikari, diurnal changes in flag leaf P_N and responses to stress were similar to those reported by Whitfield (1990); under the non-irrigated conditions the maximum P_N was attained at 06:00, and declined thereafter (Fig. 2). The early peak in P_N of non-irrigated Haruhikari is similar to that observed in wheat and other species subjected to drought (Turner *et al.* 1978, Henson *et al.* 1989, Puech-Suanzes *et al.* 1989, Deng *et al.* 2000). The differences between the treatments in Haruhikari were large at 12:00, as previously observed for wheat at anthesis and grain filling stages by Deng *et al.* (2000). On the contrary, Hongmangmai maintained higher flag leaf P_N at midday under non-irrigated conditions. Therefore, differences between the two cultivars under non-irrigated conditions were more pronounced around midday, which resulted to a higher total photosynthesis during daytime in Hongmangmai than in Haruhikari.

Under drought, stomatal closure and inhibition of chloroplast activity reduce photosynthesis (Farquhar and Sharkey 1982). Stomatal closure increases the resistance to CO_2 diffusion into the leaf. An inhibition of chloroplast activity at low leaf ψ_l decreases the capacity to fix CO_2. This cannot be overcome by increasing the concentration of CO_2 (Graan and Boyer 1990). Decreasing leaf ψ_l caused a similar degree of reduction in g_s of flag leaf in Hongmangmai and Haruhikari plants (Tables 2 and 3). These observations indicated that stomatal response to declining leaf ψ_l was similar in Hongmangmai and Haruhikari, and that any differences in drought stress inhibition of P_N between these wheat cultivars cannot be fully explained by altered stomatal responses to stress. The g_s might play an important role in the high P_N under well watered or mild drought stress, but under severe drought stress the high P_N is related more to the maintenance of a higher capacity for mesophyll photosynthesis (Farquhar and Sharkey 1982, Johnson *et al.* 1987, Rekika *et al.* 1998, Shangguan *et al.* 1999). Under the non-irrigated conditions, the flag leaf of Hongmangmai maintained a lower C_i than that of Haruhikari. Arnau *et al.* (1997) and Rekika *et al.* (1998) reported that the ratio of C_i to external CO_2 concentration decreased under mild drought stress and increased under severe drought stress. Increased C_i induced by decreased g_s implicated losses in chloroplast activity because the altered chloroplast metabolism was considered to decrease the demand for CO_2 (Graan and Boyer 1990). Therefore, the lower C_i of flag leaf in non-irrigated plants of Hongmangmai indicates higher chloroplast activity to fix CO_2 than that of Haruhikari, and may be related to the high P_N of flag leaf in Hongmangmai under non-irrigated conditions.

Cultivar differences in P_N of ear in response to drought stress were also found at midday (Table 2). However, g_s and C_i of the ear showed similar reductions in non-irrigated treatment. Thus we could not characterize the relative importance of stomatal and non-stomatal factors to the decline in P_N of the ear of both cultivars.

In general, the maintenance of P_N in plants under drought stress depends on the maintenance of leaf ψ_l and/or osmotic adjustment (Morgan *et al.* 1993, Arnau *et al.* 1997, El-Hafid *et al.* 1998, Rekika *et al.* 1998, Shangguan *et al.* 1999). Some authors questioned the importance of osmotic adjustment and turgor maintenance as an adaptation to drought (Munns 1988, Girma and Krieg 1992). No marked differences in leaf ψ_l and osmotic adjustment could be observed between the two cultivars in this study (Table 3). These results suggested that Hongmangmai maintained a high P_N of flag leaf under low leaf ψ_l. Therefore, Hongmangmai seems to be a dehydration tolerant cultivar (Blum 1985).

We conclude that under drought Hongmangmai maintained higher P_N of the ear and the flag leaf during post-anthesis, which may account for the higher grain yield. It also showed higher P_N at midday under non-irrigated treatment, which resulted in a higher proportion of total photosynthesis during daytime in Hongmangmai than in Haruhikari. This higher P_N of flag leaf in Hongmangmai may be related to the greater chloroplast activity under low leaf ψ_l.

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