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Contribution of pre-anthesis assimilates and current photosynthesis to grain yield, and their relationships to drought resistance in wheat cultivars grown under different soil moisture

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Abstract

We investigated the relative importance of pre-anthesis assimilates stored in plant parts, mainly in the stem, and post-anthesis photosynthesis to drought resistance in wheat (*Triticum aestivum* L.) cultivars Hongwangmai (drought resistant) and Haruhikari (drought sensitive) subjected to two soil moisture regimes: irrigated and non-irrigated. In the irrigated treatment, soil moisture was maintained near field capacity throughout the growing season, while in the non-irrigated treatment water was withheld from 81 d after sowing until maturity. Drought stress reduced grain yield of Hongwangmai and Haruhikari by 41 and 60 %, respectively. Remobilization of pre-anthesis assimilates to the grain (remobilization) was reduced by drought in Hongwangmai but increased in Haruhikari. The contribution of pre-anthesis assimilates to the grain decreased under non-irrigated treatment in Hongwangmai. However, under water stress, Hongwangmai maintained a higher net photosynthetic rate in the flag leaf than Haruhikari. These results indicated that maintenance of post-anthesis photosynthetic rate was related to drought resistance in Hongwangmai rather than to remobilization under drought stress.

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

Introduction

Grain formation and development in wheat depend on carbon from three sources: current assimilation, remobilization of pre-anthesis assimilates stored mainly in the stem, and re-transportation of assimilates stored temporarily in the stem after anthesis (Kobata *et al.* 1992). Under drought, there is a rapid decline in photosynthesis after anthesis, limiting the contribution of current assimilates to the grain. Drought increases the portion of the grain matter originating from stem reserves, with values ranging from near 10 % under normal conditions to greater than 40 % when drought or heat stress occurs (Rawson and Evans 1971, Austin *et al.* 1977, Bidinger *et al.* 1977, Aggarwal and Sinha 1984, Davidson and Chevalier 1992, Palta *et al.* 1994, Ehdaie and Waines 1996, Yang *et al.* 2000). Genotypic variation exists for various aspects of grain filling from stem reserves, but the relationship between the contribution and the drought tolerance is not well understood.

Under favourable conditions approximately 70 to 90 % of the final grain yield is derived from photosynthates made during the grain filling periods (Austin *et al.* 1977, Bidinger *et al.* 1977). The flag leaf usually contributes most of the photosynthates to the grain (Evans *et al.* 1972, Austin *et al.* 1977, Makunga *et al.* 1978). Thorne (1973) reported that about 60 % of the grain saccharides are derived from photosynthates in the flag leaf, suggesting that photosynthate production by the flag leaf during grain filling may limit the grain growth. On the contrary, some experimental data on wheat have indicated that inter-specific difference in grain yield is not necessarily related to differences in leaf photosynthesis (Gent and Kiyomoto 1985). However, most of the previous studies were conducted under favourable soil moisture conditions. Wada *et al.* (1994) found a positive correlation between leaf photosynthesis and grain yield only in non-irrigated treatment.

The effects of drought on photosynthesis are well documented (*e.g.* Kaiser 1987, Chaves 1991). While most

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of the drought-mediated reduction in CO_2 assimilation was attributed to stomatal closure, a part of it was attributed to the direct effect of water stress on the inhibition of CO_2 fixation (Sharkey and Seemann 1989). The relative magnitude of stomatal and non-stomatal factors in limiting photosynthesis depends on severity of the stress (*e.g.* Kicheva *et al.* 1994). Little is known about the current photosynthesis and the remobilization of reserves during grain filling.

Hongwangmai is a popular local cultivar in the Loess Plateau, China (Inanaga 1989). It is a drought resistant cultivar, able to produce better yield than other cultivars under drought. The objective of this study was to document the contribution of pre-anthesis assimilates and post-anthesis photosynthesis to grain yield of two wheat cultivars under water deficit. We also studied their influence on the drought resistance of Hongwangmai.

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 2001 to June 2002. 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 replicates. The main-plots consisted of irrigated and non-irrigated treatments. The sub-plots consisted of two tall wheat cultivars: Hongwangmai, a drought resistant local cultivar grown in the Loess Plateau, China and Haruhikari, a Japanese cultivar with high yielding potential under favourable conditions. Sub-plots were separated by plastic plates, vertically buried to a depth of 60 cm.

Seeds were sown on 28 November 2001 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 17 February 2002, water stress treatment was initiated by withholding water from non-irrigated plots until maturity. On the other hand, 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 2 April (43 d after treatment, DAT), 27 April (68 DAT), 6 May (77 DAT), 14 May (85 DAT), 24 May (95 DAT), and 29 May (100 DAT). The net photosynthetic rate (P_N), stomatal conductance (g_s), and intercellular CO_2 concentration (c_i) were measured with a portable photosynthesis system *LI-6400* (*LI-COR*, Lincoln, USA) on the uppermost fully expanded leaves from randomly selected plants. Photosynthetically active radiation (PAR) of 1 800 µmol m^{-2} s^{-1} was provided at each measurement by the *6400-02* Light Source. Leaf water status was measured near midday on 6 May (77 DAT). A pressure chamber (model *1000*, *PMS,* Oregon, USA) was used for leaf water potential (ψ_l) measurements. Leaf relative water content (RWC) was determined as described by Kobata (1984).

Aboveground biomass was taken at the initiation of treatment, at anthesis, and at physiological maturity. Leaf area was measured at anthesis 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 matter recorded.

Various parameters describing the dry matter (DM) mobilization within the plant were evaluated as follows:

Remobilization [g m^{-2}] = shoot dry matter at anthesis – (shoot – grain) DM at maturity.

Contribution of pre-anthesis assimilates to grain [%] = (remobilization/grain yield)×100.

Analysis of variance was used to analyze the experimental data.

Results

There were significant cultivar effects on LAI at anthesis ($p<0.001$), grain yield ($p<0.05$), total shoot DM at maturity ($p<0.05$), and DM accumulation from anthesis to maturity ($p<0.05$) (Table 1). There were highly significant treatment effects for all parameters shown in Table 1 except remobilization. Interaction effects were significant for all characters studied. An opposite trend was noted in the remobilization in the two cultivars. Whereas a marked increase in the remobilization was observed for Haruhikari, a 92 % decrease was recorded for Hongwangmai.

Non-irrigated treatment greatly increased remobilization in Haruhikari, but decreased it in Hongwangmai. A similar result was obtained for the per cent contribution of pre-anthesis assimilates to the grain. Under non-irrigated condition, this contribution was markedly reduced in Hongwangmai, but reached 109 % in Haruhikari. Grain yield of both cultivars was decreased by soil drying, with more pronounced effects on Haruhikari.

At anthesis, total shoot DM and LAI of both cultivars declined under soil drying (Table 1), but reductions were more severe in Hongwangmai. In contrast, total shoot DM at maturity under non-irrigated condition decreased by 54 % in Hongwangmai and by 67 % in Haruhikari relative to irrigated treatment. Thus, the two cultivars

Table 1. Leaf area index (LAI), total shoot dry matter (DM) and grain DM [g m^{-2}], DM accumulation from anthesis to maturity [g m^{-2}], remobilization of pre-anthesis assimilates to the grain [g m^{-2}], and its contribution to the grain of two wheat cultivars grown under two soil moisture levels [%]. NS, *, **, ***; not significant, significant at 5.0, 1.0, and 0.1 % levels, respectively.

Cultivar	Treatment	Anthesis LAI	 DM	Maturity Grain	 DM	DM accumulation	Remobilization	Contribution
Hongwangmai	Irrigated	2.9	912	291	1037	125	166	56
	Non-irrigated	0.8	315	171	473	158	13	8
Haruhikari	Irrigated	1.9	794	378	1236	442	–63	–16
	Non-irrigated	0.6	426	150	413	–13	163	109
Variation source	Cultivar	***	NS	*	*	*	NS	NS
	Treatment	***	***	***	***	***	NS	**
	Interaction	**	*	**	***	***	***	***

Table 2. Influence of irrigation treatment on flag leaf xylem water potential (ψ_l) and relative water content (RWC) of two wheat cultivars on 6 May (77 d after treatment). NS, *, **, ***; not significant, significant at 5.0, 1.0, and 0.1 % levels, respectively.

Cultivar	Treatment	ψ_l [MPa]	RWC [%]
Hongwangmai	Irrigated	–1.52	84
	Non-irrigated	–2.77	75
Haruhikari	Irrigated	–1.57	89
	Non-irrigated	–2.42	72
Variation source	Cultivar	NS	NS
	Treatment	***	**
	Interaction	NS	NS

differed markedly with respect to the change in aboveground DM between anthesis and maturity. In Hongwangmai, there was no significant increase in DM accumulation from anthesis to maturity for the irrigated and non-irrigated treatments, whereas the DM in Haruhikari remarkably increased in irrigated treatment after anthesis and was little changed under non-irrigated treatment.

The P_N of both cultivars under non-stress conditions was significantly higher than under water stress (Fig. 1*A*). The values dropped gradually after anthesis to nearly half prior to anthesis. Under non-irrigated conditions, P_N of Hongwangmai was higher than that of Haruhikari and remained nearly unchanged throughout the period of measurement; water stress reduced P_N by 40 % in Hongwangmai and by 77 % in Haruhikari at 77 DAT, and P_N in Haruhikari exhibited a gradual decline up to 4.0 µmol m^{-2} s^{-1} at 85 DAT.

Similar to P_N, values of g_s in irrigated treatment were significantly higher than under water stress (Fig. 1*B*). In irrigated treatment, g_s of both cultivars peaked at 68 DAT, then decreased rapidly to nearly their original values at 77 DAT and thereafter remained relatively unchanged. The g_s of plants under water stress was nearly the same on all sampling dates. Irrespective of treatment, Hongwangmai exhibited higher g_s than Haruhikari after anthesis. The difference, however, was less pronounced under water stress.

The c_i showed a similar trend with P_N and g_s in irrigated treatment, but not under water stress (Fig. 1*C*). In the latter treatment, it changed only slightly until 77 DAT, and rose thereafter. The c_i was significantly higher in the irrigated treatment than in the non-irrigated treatment until 77 DAT, but showed no strong differences thereafter. There were no significant differences in c_i between the two cultivars at 77 DAT.

The ψ_l and RWC of the flag leaves at 77 DAT were significantly higher in the irrigated treatment than in the non-irrigated treatment (Table 2). There were no significant differences in ψ_l and RWC between the two cultivars.

Discussion

The grain yield of Hongwangmai was less affected by water stress than that of Haruhikari (Table 1). Total shoot DM also decreased under non-irrigated treatment in both cultivars, with more pronounced effect on Haruhikari. This reduction could be related to low DM accumulation from anthesis to maturity in Haruhikari due to stress-induced limitation in P_N.

The two cultivars responded differently to water stress with respect to the remobilization and its contribution to grain yield (Table 1). Hongwangmai relied on considerable pre-anthesis assimilates for grain filling under irrigation. In contrast, Haruhikari did not remobilize pre-anthesis assimilates for grain filling. It seemed that post-anthesis photosynthesis satisfied assimilate requirement for grain filling in Haruhikari, but not in Hongwangmai under irrigated treatment. When water stress was imposed, however, Hongwangmai remobilized little pre-anthesis assimilates for grain filling, while Haruhikari relied heavily on pre-stored assimilates to fill the grain.

Under optimum conditions of water availability and temperature, the contribution of pre-anthesis assimilates to grain filling is very small (Thorne 1966, Wardlaw and

Porter 1967, Rawson and Evans 1971, Austin *et al.* 1977). The contributions become greater when plants are grown under drought stress than under irrigation (Bidinger *et al.* 1977, Aggarwal and Sinha 1984). Water deficits do not enhance the remobilization (Rawson *et al.* 1977). Aggarwal and Sinha (1984) observed that a drought tolerant cultivar substantially mobilized more pre-anthesis assimilates both under the irrigated and non-irrigated conditions than a moderately tolerant variety. A similar result was obtained with Haruhikari which mobilized more pre-anthesis assimilates under water stress. However, the drought resistant Hongwangmai reduced the contribution of pre-anthesis assimilates to grain filling, probably due to its ability to maintain post-anthesis assimilates (Table 1). This finding is contrary to the belief that droughted plants may remobilize more pre-anthesis assimilates to fill their grains. In relative terms this may well be the case, but our data suggest this is not so in absolute terms.

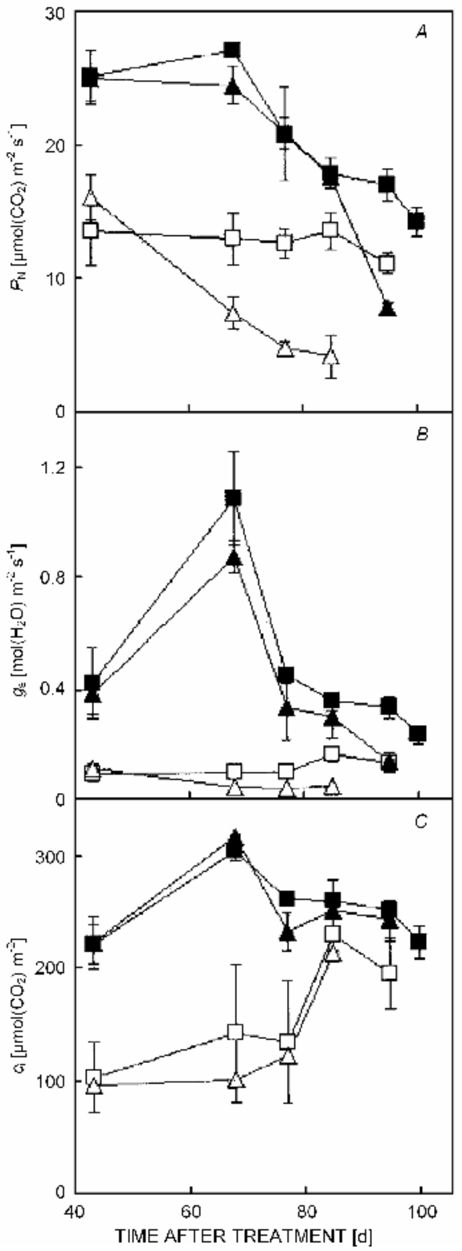

Fig. 1. Net photosynthetic rate, P_N (*A*), stomatal conductance, g_s (*B*), and intercellular CO$_2$ concentration, c_i (*C*) of the uppermost fully expanded leaves of two wheat cultivars grown in irrigated and non-irrigated treatments. ■ – Hongwangmai, irrigated; □ – Hongwangmai, non-irrigated; ▲ – Haruhikari, irrigated; Δ – Haruhikari, non-irrigated. *Bars* indicate ±SE of the mean where values exceed the size of the symbol.

The DM accumulation from anthesis to maturity was almost similar in Hongwangmai irrespective of the treatment (Table 1). In contrast, Haruhikari did not assimilate after anthesis in non-irrigated treatment but showed the greatest amount of post-anthesis assimilates in the irrigated treatment. Therefore, the contributions of remobilization may be related to the post-anthesis assimilates.

Approximately 70–90 % of the grain DM comes from photosynthates made during the grain filling period (Austin *et al.* 1977, Bidinger *et al.* 1977). Thorne (1973) reported that about 60 % of the saccharides of the grain were derived from photosynthates in the flag leaf. Only when prolonged periods of water stress occur during grain filling did photosynthates made prior to anthesis became a significant part of grain yield (Bidinger *et al.* 1977). Therefore, the photosynthates produced by the flag leaf during grain filling may limit the growth of grain.

Under water stress, P_N of flag leaf was significantly higher in Hongwangmai than Haruhikari during grain filling (Fig. 1*A*). Rawson *et al.* (1983) demonstrated that the decline in P_N of upper leaves with age was linear with time. Our observation also showed that P_N of the flag leaves declined with age in Haruhikari, but not in Hongwangmai. The latter cultivar maintained fairly high P_N during post-anthesis periods under water stress. Under this condition, g_s was more affected than P_N (Fig. 1*A,B*). A similar result was observed by Rekika *et al.* (1995, 1998). There were no significant differences in g_s and c_i between the studied cultivars (Fig. 1*B,C*), as previously observed in six barley genotypes by Arnau *et al.* (1997). However, El Hafid *et al.* (1998a) reported that drought susceptible genotypes exhibited lower g_s than tolerant genotypes upon exposure to the stress.

The decrease in P_N in water-stressed plants could be explained by the stomatal closure, which reduced CO$_2$ diffusion and thus c_i. The c_i under water stress showed either lower or similar values relative to irrigated treatment during the grain filling. This implies that stomatal closure may be responsible for water stress-induced reduction in P_N rather than non-stomatal factors. These results contradict the recent view that an early decrease in photosynthesis under drought is due to increased stomatal resistance, whereas continued water deficit causes an apparent damage to the mesophyll and consequently a reduction in photosynthetic activity (Kicheva *et al.* 1994, El Hafid *et al.* 1998b). According to Chaves (1991), however, under moderate water stress CO_2 assimilation is inhibited mainly as a result of stomatal closure, and carbon assimilation may drop to zero without affecting the photosynthetic apparatus.

No significant differences between cultivars were observed in ψ_l and RWC of flag leaves (Table 2). El Hafid *et al*. (1998a) observed that under severe drought, water content of the leaves of the drought susceptible cultivars of wheat showed a greater decline to reach a lower water potential than those of drought resistant cultivars. Our results did not show any difference in leaf water relations between the cultivars, though P_N of Hongwangmai was significantly higher than that of Haruhikari.

Drought resistance is a general term and could refer to any of several responses such as drought escape, dehydration avoidance, or dehydration tolerance (Blum 1985). The plant with dehydration tolerance is able to maintain a relatively high photosynthesis under low ψ_l induced by low soil water potential. Therefore, Hongwangmai seems to be a dehydration tolerant cultivar. There were no cultivar differences in g_s and c_i in response to water stress. It is not clear yet whether the stomatal or non-stomatal factors contribute to the maintenance of photosynthesis under drought in Hongwangmai. Further research is needed to understand the mechanisms that enable Hongwangmai to adapt to water stress.

In conclusion, Hongwangmai depended less on pre-anthesis assimilates under drought stress compared with the sensitive cultivar Haruhikari, because it was able to maintain a higher P_N during grain filling periods. The trait would account for the greater dehydration tolerance of Hongwangmai. Such traits might benefit wheat production in regions where drought stress is a common phenomenon during grain filling.

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