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Wheat Cultivar Differences in Photosynthetic Response to Low Soil Water Potentials

I. Maintenance of photosynthesis and leaf water potential

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Abstract : Although many studies have shown cultivar differences in photosynthetic response to water deficit, the understanding of detailed mechanisms is not sufficient. We examined the mechanisms of water stress-resistance in terms of photosynthetic performance under low soil water potential (Ψ_{soil}) with sixteen cultivars of wheat (*Triticum aestivum* L.) from different habitats, which had shown different drought resistance on a grain yield basis. Cultivar differences in photosynthetic maintenance in response to decrease of Ψ_{soil} (water stress resistance), were found at all seedling, booting, and grain filling stages. Cultivars with high drought resistance based on grain yield also showed high water stress resistance in photosynthetic performance. Water stress resistance (R_{WS}) was caused more by tolerance (T_{WS}, maintenance ability of photosynthesis in response to decrease of leaf water potential, Ψ_L) in some cultivars, which maintained relatively high photosynthesis (P_N) in spite of decreases in Ψ_L, while it was caused more by water stress avoidance (A_{WS}, maintenance ability of Ψ_L in response to decreases in Ψ_{soil}) in other cultivars, which showed a relatively high P_N by maintaining a relatively high Ψ_L under the same low Ψ_{soil}. However, there was a positive correlation between R_{WS} and T_{WS} or between R_{WS} and A_{WS}. It is suggested that avoidance and tolerance usually occur simultaneously in adaptation to low Ψ_{soil}, although water stress resistant cultivars varied in the water stress resistance mechanism.
Key words : Drought avoidance, Drought resistance, Drought tolerance, Photosynthesis, *Triticum aestivum*, Water stress, Wheat.

コムギにおける光合成の低土壌水ポテンシャルに対する反応の品種間差　第１報　光合成および葉の水ポテンシャルの維持能力：徐　会連・石井龍一（東大大学院農学生命科学研究科）

要　旨：水欠乏に対する光合成の反応に品種間差があることは知られているが，そのメカニズムにはまだわからないことが多い．本研究は，収量の上で耐乾燥性が異なる品種について，土壌の水ポテンシャル(Ψ_{soil})の低下に対する光合成の反応の品種間差を調べることによって，コムギにおける光合成の水ストレスに対する抵抗性のメカニズムを検討したものである．Ψ_{soil} の低下に対する光合成の反応の品種間差は，幼植物期，穂ばらみ期，稔実期のいずれの生育期においても認められた．収量の面で耐乾燥性が強い品種は光合成の面でも Ψ_{soil} の低下に対して強かった．水ストレスに強い品種の中には，Ψ_{soil} の低下に伴ってその葉の水ポテンシャル(Ψ_L) も低下するが，そうした低い Ψ_L 下でも高い光合成活性を保つことができる水ストレス耐性の高い品種と，Ψ_{soil} が低下しても Ψ_L の低下を抑えることによって，高い光合成活性を保つことができる水ストレス回避性が高い品種とがあることがわかった．しかし，全体の品種についてみると，水ストレス抵抗性，耐性と回避性の３者の間には相互に正の相関が認められ，水ストレス耐性と回避性とは，乾燥環境に適応するため同時に形成された水ストレス抵抗性の構成要素であると考えられた。
キーワード：乾燥回避性，光合成，コムギ，乾燥耐性，水ストレス．

With a few exceptions, technologies have not been developed to allow many physiological mechanisms to be routinely evaluated with large numbers of plants at one experiment. Some specific characteristics should be chosen as indicators, for an example, of drought resistance. Drought resistance usually refers to the ability of plants to survive in water deficit conditions in ecological researches[14,17], and to maintain economic yield performance under drought conditions in agronomical studies [1,11,15,21]. Photosynthesis is one of the most fundamental physiological processes associated with both survival and yield under drought conditions. Therefore, in the recent study we used photosynthetic maintenance ability under low soil water potentials (Ψ_{soil}) as one of the indicators of drought resistance. For many crops, photosynthetic capacity shows a high positive correlation with grain yield only under drought conditions[10,11,19]. For an example, Fischer and Turner[10] and Wada et al.[19]

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have reported that a positive correlation between photosynthetic rate and grain yield of wheat was found under drought conditions but not under irrigated conditions. Therefore, photosynthetic rate under water deficit conditions is one of the important indicators of drought resistance.

A cultivar may use a multiplicity of tolerance and/or avoidance mechanisms to achieve a measure of overall drought resistance in given soil water conditions. Therefore, we analyzed the mechanisms of photosynthetic maintenance of various wheat cultivars under artificial water deficit conditions in terms of tolerance and avoidance following the ideas of Levitt's[13]. Since "drought" is a meteorological term, and is commonly defined as a period without significant rainfall, we substitute "water stress resistance" for "drought resistance" as proposed by Ludlow et al[16]. It is well documented that a low Ψ_{soil} induces a decrease in leaf water potential (Ψ_L) together with a decrease in leaf turgor potential and leaf water content, resulting in a photosynthetic depression by stomatal closure and inhibition of enzyme activity [2,3,5,6,7,8,12,19]. In such cases, the plant is considered to be stressed by water deficit, i.e., water stressed conditions. In the present study, if a cultivar shows the ability to maintain a high photosynthetic activity under low Ψ_{soil} no matter how much Ψ_L decreases, the plant was considered to be water-stress resistant. Water stress resistance, in a broad sence, is the general term used to cover a wide range of mechanisms by which plants withstand water stress conditions[14,16]. In order to approach the mechanism of water stress resistance, we separated water stress resistance into its two components, tolerance and avoidance, following the ideas of Levitt's[13] and Ludlow et al[16]. A plant with water stress avoidance can maintain a relative high Ψ_L under low Ψ_{soil} and consequently maintains relatively high photosynthesis. The plant with water stress tolerance is able to maintain a relatively high photosynthesis under low Ψ_L induced by low Ψ_{soil}. Therefore, water-stress resistance, by definition, is the total ability of plants to endure water stress conditions, either caused by avoidance or by the tolerance mechanism.

In the present study, 16 cultivars originally from Brazil, China, and Japan were examined. Drought resistance based on grain yield for the Brazilian cultivars used here has been confirmed by other researchers[19]. Some of the Chinese cultivars have been used as drought resistant varieties in Northwest China. In the work, we only examined photosynthetic maintenance under low Ψ_{soil} and the related mechanisms.

Materials and Methods

Plant materials and soil water treatment

Plant materials used here were 16 cultivars of common wheat (*Triticum aestivum* L.) from different habitats, China, Japan and Brazil, having different agronomic drought resistance as shown in Table 1 (Wada et al., 1994; Wang, 1985, personal communication). One Wagner pot with 1/5000 a of soil surface area contained 8 plants each from different cultivars. Another 8 cultivars were raised in another pot. Therefore, two pots of plants were one unit of cultivar treatments. Six g of compound fertilizer (14-20-14) was applied per pot. In the next spring, pots were transferred into a natural light glasshouse, where the air temperature, and relative humidity were controlled at 25/20°C (day/night), and 60%, respectively. Experiments were carried out at seedling, booting, and grain filling stages. Before starting the soil water treatment, all pots were watered to saturation. Different Ψ_{soil} was obtained by stopping the water supply at different times within 6 days. The pots with water supply first stopped had the lowest Ψ_{soil}, while the pots for which water supply stopped later showed higher Ψ_{soil}. There was no re-irrigation to any treatment of soil water content because it was not easy to distribute the re-irrigated water evenly in the whole pot. Measurements of photosynthesis and Ψ_L were made just after the pot reached the designed Ψ_{soil}.

Determinations of soil and leaf water potentials

Since it is inconvenient to determine Ψ_{soil} at the photosynthetic measurement time, the regression between soil water content and Ψ_{soil} was determined beforehand in the laboratory using a psychrometer (Wescor RH52). Soil water content was deternined by weighing the pot at the time of photosynthetic measurement and then Ψ_{soil} was calculated from the regression between soil water content and

Ψ_{soil} ($\Psi_{soil}=89.3934\ e^{-0.0922686x}$, $r^2=0.92$). Ψ_L was measured by the pressure chamber method after photosynthetic measurement. The fully expanded 6th leaf from the base at seedling stage, or the flag leaf at booting and grain filling stages was excised, immediately sealed in a small polyvinyl bag, and then mounted in the pressure chamber for measurement. The speed of the pressure application was relatively fast at the beginning and lowered down to 0.01 MPa s^{-1} when the pressure closed to the Ψ_L. The values of Ψ_L obtained by the pressure chamber (x) were calibrated to those obtained by a psychrometer (y) (Wescor RH52) in the laboratory ($y=0.88x$ for all cultivars).

Photosynthetic measurement

Net photosynthetic rate (P_N) was determined with a portable photosynthesis-transpiration measurement system (Koito KIP-8510) under a constant photosynthetic photon flux of $800\pm50\ \mu$mol m^{-2} s^{-1}. The air temperature in the assimilation chamber was 24 ± 1°C, and CO_2 concentration in air from the inlet was 380 ppm. The vapor pressure deficit between the leaf and air in the assimilation chamber was 1.2 ± 0.14 kPa with fluctuations. All measurements were made using the fully expanded 6th leaf at seedling stage and the flag leaf at booting and grain filling stages.

Determination of water stress resistance, tolerance and avoidance

According to concepts of Levitt's[13] and Ludlow et al[16], water stress resistance (Rws), which was defined as the ability of photosynthetic maintenance under low Ψ_{soil}, was expressed by the absolute value of Ψ_{soil} at which P_N was depressed to the level of 50% of the value in non-stressed plants. Water stress tolerance (T_{WS}), which was defined as the ability of photosynthetic maintenance under low Ψ_L, was expressed by the absolute value of Ψ_L at P_N decreased by 50%. Drought avoidance (A_{WS}), which was defined as the ability of Ψ_L maintenance under low Ψ_{soil}, was expressed by the ratio of R_{WS} to T_{WS}. Here, $R_{WS}/T_{WS}=1$ means that Ψ_L reached the equilibrium with Ψ_{soil} but it is impossible on a theoretical and neither on a practical basis, and therefore, the ratio is less than 1. The definitions of the above-mentioned R_{WS}, T_{WS}, and A_{WS} were based on half inhibition or percentage inhibition. Therefore, the abilities of photosynthetic maintenance could be compared on a relative basis no matter how large or small the initial maximum P_N was.

Results

Cultivar difference in water stress resistance

Table 1 shows the regression coefficient between P_N and Ψ_{soil} given by $P_N=a+b\Psi_{soil}+c\Psi^2_{soil}$ with the P_N value at -0.8 MPa of Ψ_{soil} for each cultivar at seedling, booting and grain filling stages. The cultivars were listed in the order of $P_{0.8}$ (P_N value at -0.8 MPa of Ψ_{soil}). The characteristics of the regression curve can be shown by the coefficients, a, b, and c. Some examples at seedling stage in Table 1 are visually shown by Fig. 1. $P_{0.8}$ is dependent on both decreasing rate and the initial maximum value (P_{max}). For an example, Sumai 3 showed a larger decreasing rate of P_N with a higher P_{max} and a lower $P_{0.8}$ than the cultivar 78 (13)-3. The cultivar BH 1146 showed a larger decreasing rate of P_N with a higher P_{max}, but a higher $P_{0.8}$ than cultivars Sumai 3 and 78 (13)-3.

Table 2 shows the regression coefficients between Ψ_L and P_N as well as $P_{1.5}$ (the P_N value at -1.5 MPa of Ψ_L) for each cultivar. There were also differences among cultivars in the coefficients and $P_{1.5}$. The examples in Fig. 2 help understand the regression in different cultivars. Norin 61 had a higher P_N at high Ψ_L and a lower P_N at lower Ψ_L than 78 (13)-3. Gammai 11 and 78 (13)-3 showed different P_N at high Ψ_L, but a similar P_N at low Ψ_L. Moreover, the ranking order of $P_{1.5}$ was not the same at $P_{0.8}$ in Table 1.

In Table 3, R_{WS}, T_{WS} and A_{WS} were shown together with P_{max}. Here, the cultivars were listed in the order or R_{WS} at seedling stage. It should be noticed that, at seedling stage, the Chinese local cultivars (from Hongmang to Dabaimang) are located in high rank, but Chinese new cultivars (from Sumai to Keyi 26) are in the last ones. Brazil cultivars (BR 9, BR 8 BH 1146) are in the middle, and Japanese cultivars (Norin 61 and Asakaze) are in relatively low rankings. The order of R_{WS} changed a little as the growth stage developed. However, cultivar differences in R_{WS}, T_{WS} and A_{WS} were apparent in all stages.

By precisely analyzing the mechanism of water stress resistance by comparing the val-

Table 1. Regression coefficients in the relationship, given as $y=a+bx+cx^2$, between photosynthetic rate potential (x, MPa) at seedling, booting, and grain filling stages, with the photonynthetic rate at −0.8

Cultivar	Seedling stage					Booting stage				
	a	b	c	r^2	$P_{0.8}$	a	b	c	r^2	$P_{0.8}$
71-321 (China) +	20.8	15.3	−3.0	0.92	6.6	17.6	−7.1	−7.9	0.94	6.9
Hongmang (China) +	13.6	3.3	−8.3	0.90	5.7	16.4	−14.3	0.0	0.85	4.9
78 (13) -3 (China)	13.0	4.1	−6.8	0.88	5.4	16.1	−4.9	−7.6	0.88	7.3
Hongmangbai (China) +	13.4	4.3	−7.1	0.90	5.4	13.8	5.5	15.8	0.98	8.1
Gammai 11 (China) +	16.7	6.9	−9.3	0.90	5.2	18.4	−12.7	0.0	0.98	8.3
BH 1146 (Brazil) +	19.9	17.9	0.0	0.83	5.6	21.4	−19.1	0.0	0.96	6.2
Bimai 5 (China) +	18.6	16.9	0.0	0.85	4.9	19.3	−18.0	0.0	0.92	4.9
Debaimang (China) +	17.2	12.5	−3.9	0.88	4.8	14.7	1.4	−10.9	0.96	8.9
BR 10 (Brazil) −	19.8	10.9	−2.3	0.90	4.6	20.2	−34.2	17.5	0.94	4.1
BR 9 (Brazil) +	16.7	16.8	0.0	0.83	3.3	17.5	5.9	20.4	0.96	9.1
BR 8 (Brazil) +	16.7	16.8	0.0	0.85	3.3	21.4	0.3	22.8	0.98	7.1
Keyi 26 (China)	16.8	55.1	−7.3	0.94	2.6	18.8	−35.3	17.9	0.96	2.1
Asakaze (Japan)	17.8	27.7	10.7	0.92	2.4	25.0	−39.4	18.9	0.96	5.6
Wangmai 17 (China) −	17.7	27.6	10.6	0.90	2.4	20.7	−38.9	23.4	0.96	2.6
Norin 61 (Japan)	19.0	30.0	10.6	0.88	1.9	22.3	−25.1	8.9	0.96	7.4
Sumai 3 (China) −	18.9	31.1	11.8	0.96	1.6	22.0	−38.1	16.4	0.94	2.1

Original habitat of the cultivar is shown in parenthesis. The scripts, + and − mean agronomically drought

Table 2. Regression coefficients in the relationship, given as $y=a+bx+cx^2$, between photosynthetic rate potential (x, MPa) at seedling, booting, and grain filling stages, with the photosynthetic rate at −1.5

Cultivar	Seedling stage					Booting stage				
	a	b	c	r^2	$P_{1.5}$	a	b	c	r^2	$P_{1.5}$
71-321	22.3	5.8	−2.1	0.86	9.0	18.6	−0.5	−4.0	0.94	8.8
Gammai 11	17.3	0.9	−3.9	0.88	7.3	22.8	−10.3	0.0	0.96	7.4
BR 9	21.1	5.9	−2.4	0.86	7.3	16.4	5.6	−5.4	0.90	12.7
78 (13) -3	12.6	1.6	−3.5	0.85	7.3	16.6	0.5	−4.0	0.96	8.6
Bimai 5	22.3	10.6	0.0	0.85	6.4	26.9	−12.7	0.0	0.92	7.8
Hongmangbai	14.1	0.9	−3.3	0.88	5.5	6.9	−21.1	14.9	0.98	4.9
BH 1146	24.8	13.1	0.0	0.83	5.1	25.8	−11.8	0.0	0.96	8.1
Wangmai 17	19.8	9.8	0.0	0.85	5.1	39.4	−41.3	11.8	0.94	3.6
BR 8	19.8	9.9	0.0	0.83	5.1	20.0	6.9	8.5	0.96	9.4
BR 10	20.1	10.0	0.0	0.86	5.1	38.6	−39.1	10.5	0.92	3.6
Hongmang	14.5	0.1	−4.4	0.88	4.5	23.8	−13.8	0.0	0.85	7.1
Debaimang	19.5	5.6	−3.1	0.92	4.1	11.1	11.6	−9.4	0.96	7.3
Keyi 26	20.7	13.3	1.5	0.85	4.1	34.0	36.2	10.1	0.96	2.4
Asakaze	22.7	15.9	2.4	0.96	4.1	41.8	−32.6	7.1	0.92	8.8
Norin 61	24.0	16.6	2.3	0.90	4.1	31.5	−18.8	3.2	0.96	10.4
Sumai 3	20.9	11.2	0.0	0.85	4.1	31.4	−25.3	5.1	0.94	4.9

ues of T_{WS} and A_{WS}, for example at seedling stage, we found that R_{WS} of Hongmangbai is more contributed by T_{WS} compared with 78 (13)-3. T_{WS} is higher and A_{WS} is lower in Hongmangbai than in 78 (13)-3, although they have almost the same R_{WS} value. This suggests that the mechanism of water stress resistance is different with cultivars. Similar example can be taken from the data at booting stage. BR 9 and Hongmangbai were the same in R_{WS}, but different in T_{WS} and A_{WS}. The mechanistic analysis was shown in Fig. 3. BR

(y, μmol $m^{-2}s^{-1}$) and soil water
MPa of soil water potential ($P_{0.8}$).

Grain filling stage				
a	b	c	r^2	$P_{0.8}$
19.6	−12.1	−7.8	0.94	4.9
19.6	−17.4	0.0	0.94	5.8
17.1	−6.7	−8.8	0.94	6.1
17.9	−13.6	0.0	0.81	7.1
17.9	−1.0	−15.0	0.88	7.4
18.0	4.9	−23.0	0.90	7.3
17.4	7.8	−7.8	0.88	6.6
15.3	2.6	−18.5	0.86	5.4
20.1	−32.6	20.1	0.90	6.9
18.4	3.1	−21.2	0.92	7.4
21.1	1.4	−21.7	0.92	8.3
18.9	2.0	−33.3	0.90	3.9
19.4	−16.6	0.0	0.90	6.2
20.9	−25.3	6.7	0.92	4.9
20.2	−24.5	8.6	0.94	6.1
19.8	−18.6	0.0	0.90	4.8

resistant, and susceptible, respectively.

(y, μmol $m^{-2}s^{-1}$) and leaf water
MPa of leaf water potential ($P_{1.5}$).

Grain filling stage				
a	b	c	r^2	$P_{1.5}$
7.5	23.9	−12.1	0.88	16.2
16.3	4.6	3.4	0.88	15.4
33.3	−23.5	5.3	0.96	16.8
11.6	11.9	−7.6	0.87	12.8
15.8	3.8	−3.7	0.90	13.2
9.9	14.5	−7.9	0.87	13.8
4.4	24.9	−10.1	0.83	19.0
28.5	−13.0	1.2	0.98	11.6
12.7	−17.1	−8.1	0.94	19.0
8.3	19.1	8.4	0.92	18.0
15.8	6.9	5.3	0.92	14.2
4.6	22.6	−10.8	0.85	14.2
18.1	4.3	−5.1	0.88	12.6
19.0	0.9	−2.6	0.90	14.3
24.4	−7.7	0.0	0.90	12.9
24.4	−7.9	0.0	0.94	12.6

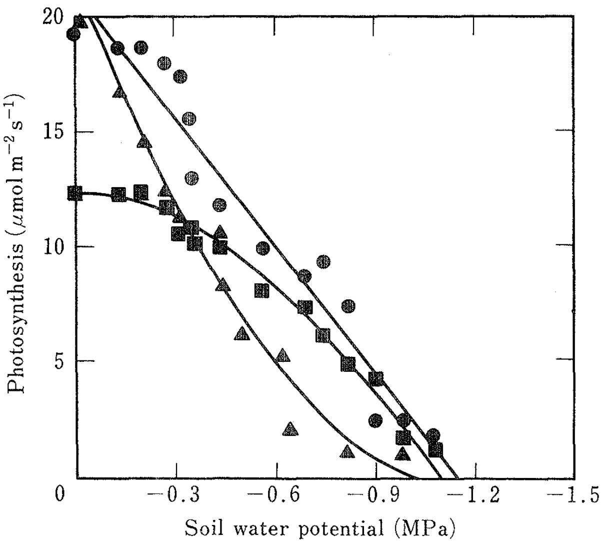

Fig. 1. Photosynthetic response to changing of soil water potential in three different cultivars, BH 1146 (●), 78 (13)-3 (■), and Sumai 3 (▲), at the seedling stage.

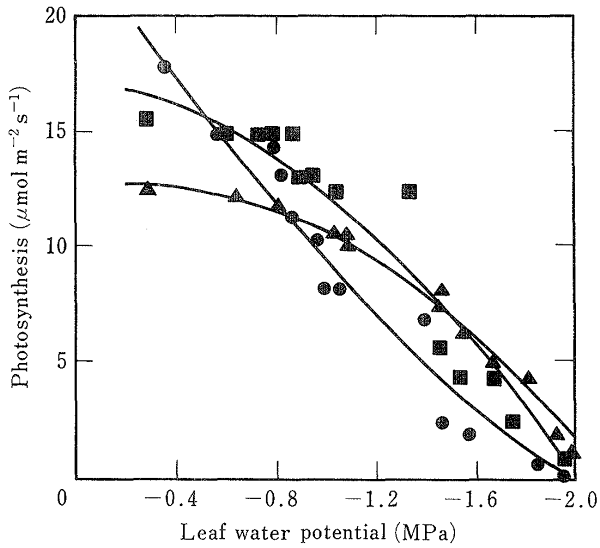

Fig. 2. Photosynthetic response to changing of leaf water potential in three different cultivars, Norin 61 (●), Gammai 11 (■), and 78 (13) -3 (▲), at the seedling stage.

9 and Hongmangbai have a similar photosynthetic response to Ψ_{soil} (Fig. 3A). However, photosynthetic response to Ψ_L was differed considerably. P_N decreased much more rapidly in Hongmangbai than in BR 9 as Ψ_L decreased (Fig. 3B). The reason for different responses to Ψ_{soil} and Ψ_L was attributable to the different maintenance of Ψ_L as Ψ_{soil} decreased (Fig. 3C). It was suggested that water stress resistance was caused more by tolerance in BR 9, which was able to maintain a relatively high P_N in spite of large decrease in Ψ_L. It was also suggested that water-stress resistance was caused more by avoidance in Hongmangbai, which was able to maintain a relatively high Ψ_L and as consequence, a relatively high P_N. Although some water stress

Table 3. Water stress resistance (R_{WS}, MPa), tolerance (T_{WS}, MPa) and avoidance (A_{WS}) as well as the maximum photosynthetic rate (P_{max}, μmol $m^{-2}s^{-1}$) of wheat plants as different growth stages.

Cultivar	Seedling stage				Booting stage				Grain filling stage			
	R_{WS}	T_{WS}	A_{WS}	P_{max}	R_{WS}	T_{WS}	A_{WS}	P_{max}	R_{WS}	T_{WS}	A_{WS}	P_{max}
Drought resistant group												
Hongmang	0.76	1.28	0.59	14.4	0.58	1.14	0.51	16.3	0.58	1.93	0.30	18.8
Hongmangbai	0.70	1.36	0.51	13.8	0.81	1.37	0.59	15.6	0.70	1.92	0.36	16.8
Gammai 11	0.67	1.45	0.46	15.6	0.70	1.29	0.54	19.4	0.73	2.26	0.32	18.1
Dabaimang	0.61	1.21	0.50	16.3	0.83	1.43	0.58	16.9	0.60	2.08	0.29	18.8
78(13)-3	0.71	1.13	0.63	12.5	0.68	1.51	0.44	16.9	0.68	1.82	0.37	16.9
71-321	0.64	1.44	0.44	19.4	0.66	1.44	0.49	18.8	0.60	1.93	0.31	17.4
Bimai 5	0.54	1.22	0.44	18.8	0.55	1.38	0.40	18.8	0.67	1.93	0.35	17.5
BH 1146	0.53	1.10	0.48	20.6	0.58	1.32	0.44	20.6	0.74	2.27	0.33	18.1
BR 9	0.47	1.13	0.42	17.4	0.79	1.79	0.44	18.8	0.73	2.21	0.33	18.8
BR 8	0.43	1.06	0.41	18.7	0.69	1.50	0.46	21.8	0.75	2.14	0.35	20.0
Mean	0.61	1.24	0.49	16.8	0.69	1.42	0.49	18.4	0.68	2.05	0.33	18.1
±SE	±0.10	±0.13	±0.06	±2.5	±0.09	±0.16	±0.06	±1.8	±0.06	±0.15	±0.02	±0.9
Drought susceptible group												
BR 10	0.57	1.36	0.42	18.1	0.30	0.98	0.31	20.6	0.46	1.58	0.29	18.7
Asakaze	0.38	1.04	0.37	17.5	0.47	1.36	0.35	21.2	0.60	2.08	0.29	18.7
Norin 61	0.38	1.04	0.37	18.1	0.54	1.45	0.37	21.9	0.48	1.83	0.26	20.7
Sumai 3	0.38	1.08	0.35	17.5	0.36	1.05	0.34	20.5	0.35	0.93	0.29	20.0
Wangmai 17	0.35	1.06	0.33	18.8	0.37	1.01	0.37	19.4	0.51	1.72	0.30	19.4
Keyi 26	0.34	1.11	0.31	15.6	0.32	0.92	0.35	18.7	0.32	0.86	0.28	19.4
Mean	0.40	1.12	0.36	17.6	0.39	1.13	0.35	20.4	0.45	1.50	0.29	19.5
±SE	±0.07	±0.11	±0.03	±1.0	±0.08	±0.20	±0.02	±1.0	±0.09	±0.45	±0.01	±0.7

resistant cultivars were different from each other in T_{WS} or A_{WS}, significant positive correlations were observed between R_{WS} and T_{WS}, or between R_{WS} and A_{WS} (Table 4). This suggests that R_{WS} is, in general, caused by T_{WS} and A_{WS} at the same time.

Changes with growth stages in water stress resistance, tolerance and avoidance

As shown in Table 1, 2 and 3, the order of photosynthetic response to Ψ_{soil} and Ψ_L i.e. the order of R_{WS}, T_{WS} and A_{WS} changes slightly as growth stage develops. The most clear and noticeable point is the order of cultivars ranked by $R_{0.8}$ and $P_{1.5}$. Brazilian cultivars raised their ranking in the grain filling stage. Two Japanese cultivars, Asakaze and Norin 61, are also located in the middle ranking in both booting and grain filling stages, although they were located near the bottom in the seedling stage. Chinese new cultivars, Keyi 26, Sumai 3, and Wangmai 17 were always located in the bottom throughout all the growth stages. The mean values of R_{WS}, T_{WS} and A_{WS} of all cultivars at three growth stages suggested that there was little change in R_{WS}, T_{WS} and A_{WS} from seedling stage to booting stage. However, at grain filling stage, T_{WS} became much larger and consequently A_{WS} was smaller than at seedling and booting stages. R_{WS} was comparatively consistent through three stages.

Correlations between three growth stages were shown in Table 4 for water stress resistance, tolerance and avoidance. Correlations were relatively high between R_{WS} and A_{WS} compared to those between R_{WS} and T_{WS}. This suggested that R_{WS} and A_{WS} were relatively stable characters through the whole life, compared with T_{WS}.

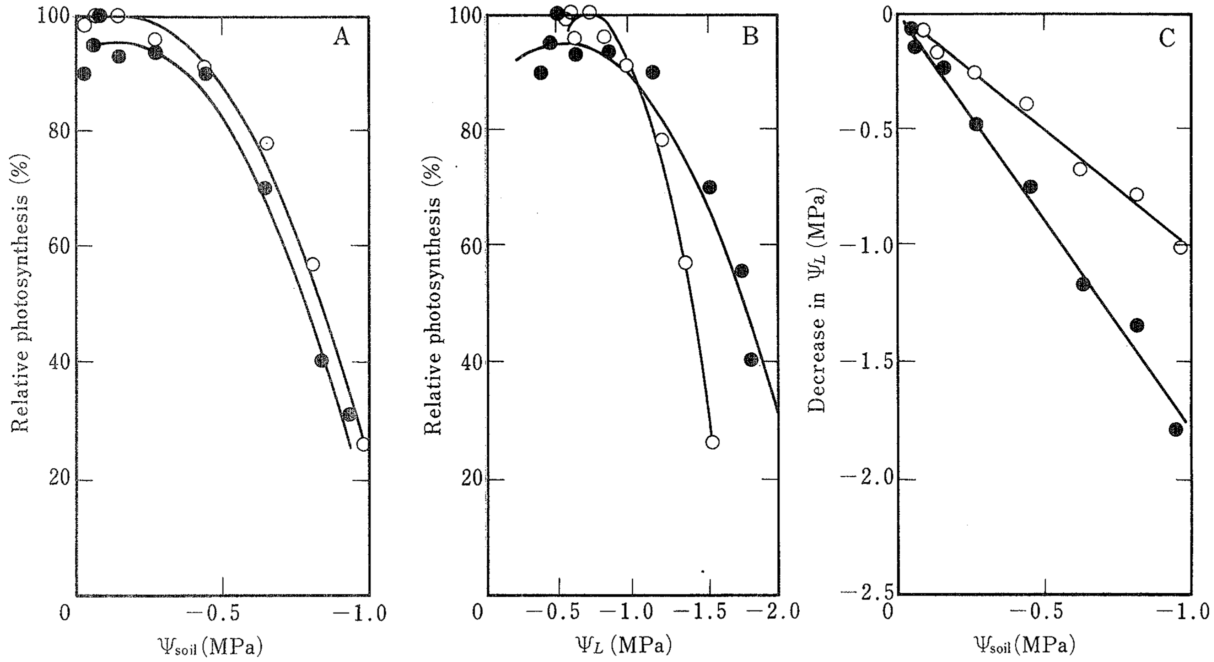

Fig. 3. Photosynthetic responses to decreases in soil and leaf water potentials and the response of leaf water potential to changing of soil water potential of a water stress tolerant cultivar, BR 9 (●), and of a water stress avoidance cultivar, Hongmangbai (○), at the booting stage.

Table 4. Correlations between the variables related to drought resistance of wheat plants.

y—x	r	y—x	r
R^S—T^S	0.74	T^G—T^S	0.26
R^S—A^S	0.90	T^G—T^B	0.70
T^S—A^S	0.39	T^B—T^S	−0.03
R^B—T^B	0.81	A^G—A^S	0.61
R^B—A^B	0.87	A^G—A^B	0.53
T^B—A^B	0.43	A^B—A^S	0.68
R^G—T^G	0.90	R^S—P^S_{max}	−0.53
R^G—A^G	0.71	R^B—P^B_{max}	−0.49
T^G—A^G	0.42	R^G—P^G_{max}	−0.56
R^G—R^S	0.54	R^S—$P^S_{0.8}$	0.90
R^G—T^B	0.84	R^B—$P^B_{0.8}$	0.91
R^B—T^S	0.61	R^G—$P^G_{0.8}$	0.75

R, T, and A mean water stress resistance, tolerance and avoidance, respectively, and the subscript, WS, is omitted here. P_{max} and $P_{0.8}$ mean the maximum photosynthetic rate and the photosynthetic rate at −0.8 MPa of soil water potential. The superscripts S, B, and G mean seedling, booting, and grain filling stages, respectively. $P_{0.05} \geq 0.48$: $P_{0.01} \geq 0.60$.

Correlation of photosynthetic rate under well-watered conditions with water stress resistance

A negative correlation was found between the maximum photosynthetic rate under well-watered conditions with water stress resistance at all three stages. This suggested that the cultivars showing a high photosynthetic rate under well-watered conditions were susceptible to water stress. The water stress resistant cultivars were able to maintain their photosynthetic activity under water stress conditions although they showed the low values of the maximum photosynthetic rate under well-watered conditions.

Discussion

As shown by Ludlow et al[16], we substituted "water stress resistance, tolerance and avoidance" for Levitt's "drought resistance, tolerance and avoidance" since our investigations were made with potted plants under controlled artificial soil water deficit conditions. Therefore, concepts of water stress adaptation used here are different from those of Levitt's. In Levitt's concept, for example, drought avoidance is due to many combinations between the different kinds of avoidance and tolerance, including soil water conservation by plant size changes or transpiration surface reduction, increases in water uptake by deep rooting in adaptation to long-term of soil water deficit, and early completion of the life cycle before severe drought season[13]. These adaptation changes do not occur in our potted plants under a short term of artificial soil water deficit. Our experiment was designed to elucidate whether a high photosynthetic maintenance of a cultivar under low Ψ_{soil} is due to the ability of maintaining a high Ψ_L, or due to tolerance ability to a low Ψ_L. Actually, no matter how low the Ψ_{soil} is, the plant is water stressed only when Ψ_L decreases to a sufficient extent. If the plant does not decrease or decreases little its Ψ_L under low Ψ_{soil}, the plant can be considered as a water stress avoider. On the other hand, if Ψ_L decreases under low Ψ_{soil} but the plant can maintain a high P_N, it can be considered to possess a water-stress tolerance mechanism.

In our experiment, we found not only cultivar differences in photosynthetic maintenance ability under low Ψ_{soil}, but also the difference in mechanisms accounting for the photosynthetic maintenance. Some photosynthetically water-stress resistant cultivars used in the present work survived with a certain level of seed yield under severe drought conditions in which other cultivars could not survive. However, Fischer[9], and Wada et al.[19] observed that high yielding capacity under well-watered conditions was positively related to susceptibility to water stress. They found no clear reason for this relationship. In the present work, it was also observed that the cultivars, such as Keyi 26, Sumai 3 and Norin 61 can perform well in grain production and photosynthetic performance under well-watered conditions, but showed large photosynthetic depression under water stress conditions.

By analyzing the mechanism, we found that the agronomically water stress resistant (based on grain yield) cultivars, such as Hongmangbai and BR 9, showed almost the same water stress resistance in photosynthesis. However, Hongmangbai showed more dependence on water stress avoidance, whereby higher Ψ_L was maintained in spite of soil water deficit, while BR 9 was more dependent on water stress tolerance, whereby higher photosynthetic activity was maintained in spite of the decrease in Ψ_L. Most of the avoidance-dependent cultivars in the present work showed a short plant type and small and narrow leaf blades (data are not provided). Furthermore, decrease in water stress avoidance at grain filling stage, as observed here, might be due to the increased shoot/root ratio and the decreased tissue water storage volume of the hollow stem. As reviewed by Levitt[13] and reported by others[16], the water stress avoidance mechanism is mainly associated with morphological characteristics. On the other hand, water stress tolerance is mainly associated with physiological characteristics[13]. Increase in water stress tolerance at grain filling stage is presumably due to increased osmotic adjustment[18,20]. Since most cultivars can carry their water stress resistance through their whole lives, by either tolerance and/or avoidance, water stress resistance defined in the present study is a consistent characteristic, and selection of water stress resistant cultivars at either of the growth stages will be possible. There might be disadvantages in pot experiments due to less space for root development. However, pot culture can provide uniform conditions to plants. In order to place all cultivars under exactly the same soil water potential, we grew several cultivars in one pot, where roots from different plants crossed with each other. Moreover, during the soil water depleting period, no re-irrigation was done and, therefore, Ψ_{soil} reached an equivalent status in the whole soil volume. Therefore, we found no local difference in Ψ_{soil} within one pot soil volume no matter how different the aboveground plant size was. In addition, pot culture is a convenient and capable means to deal with more plants compared to field experiments. Therefore, pot experiment is suitable for a drought resistant genotype selection, at least, at the beginning stage of the program. Of course, further investigations in field scale are needed to understand the full aspects of the drought resistance mechanism and confirm the results obtained in pot culture.

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