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USE OF NET PHOTOSYNTHESIS AND WATER-USE-EFFICIENCY IN BREEDING WHEAT FOR DROUGHT RESISTANCE

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Abstract

A series of experiments were conducted in pot and lysimeter conditions to evaluate net photosynthesis and water-use-efficiency as breeding criteria for drought resistance. Six drought resistant and 6 drought susceptible genotypes were used. Net photosynthesis decreased under drought which was caused mainly by non stomatal factors. Genotypes with the same stomatal conductance had different net photosynthesis under drought suggesting that genotypes with high water-use-efficiency can be tailored. Measurement of net photosynthesis and water-use-efficiency can thus be used as breeding criteria for drought resistance.

Introduction

Higher net photosynthesis (Pn) and water-use-efficiency (WUE) under drought stress have been reported as indicator for drought resistance in wheat (Dedio *et al.*, 1976; Ritchie *et al.*, 1990; Castonguay & Markhart, 1992; Johnson *et al.*, 1995). However, in earlier studies a few genotypes were compared for these traits. In the present study 12 genotypes with the same phenological development were used. Six of these genotypes were drought resistant (Pk81, Br83, Lu26S, High-ABA1, High-ABA6 and High-ABA21) and six were drought susceptible (Pb85, Fd85, Fd83, Low-ABA6, Low-ABA18 and Low-ABA21) classified on the basis of grain yield under drought observed in field and controlled condition experiments. A series of experiments were conducted under lysimeter and pot conditions to study the effect of drought stress on the traits, the response of drought resistant and susceptible genotypes for the traits and to asses the possibility of these traits to be used as drought resistance indicator to differentiate a large number of wheat genotypes or segregating populations at an early seedling stage.

Materials and Methods

Experiments were conducted at the University of Wales, Bangor, UK., during the year 1992. Randomized complete block design was followed in the experiments. In the first experiment 8 genotypes and in the other two experiments 12 genotypes were used.

Experiment 1 was conducted in a glasshouse in 12 cm plastic pots filled with 1500 g of a 1:1 mixture of air dry soil and sand. Six seeds from each of the 8 genotypes were sown in each pot and at the 3rd leaf stage three healthy seedlings were retained in each pot. There were 64 pots divided into four blocks. The seedlings were supplied with

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optimum moisture and nutrition until the 5th leaf was fully expanded. At 48 days after sowing (DAS) gas exchange measurements using infra red gas analysis system (model LCA2) were started on the 5th leaf. This instrument gives measurement of net photosynthesis, transpiration, stomatal conductance and sub-stomatal CO_2 in a single reading. Irrigation was withheld in 32 pots to develop drought stress and continued in the other 32 pots but without further nutrition. The moisture content of the soil in the pots was monitored by the filter paper method given by Fawcett & Collis-George (1967). Soil moisture was kept the same in all the pots by adding water in more stressed pots to keep a uniform rate of stress development in the genotypes. When the soil water potential reached -0.7 MPa the second measurement was made. The third measurement was made when the moisture potential of the soil approached -1.2 MPa. Twelve plants from each of the genotype were measured.

Experiment 2 was also conducted in a glasshouse. Plants were grown in 12 cm plastic pots filled with 1500 g of air dry sandy loam soil. Six seeds were planted in each pot and at the 3rd leaf stage four healthy seedlings were left in each pot. There were 48 pots divided into four blocks with four pots for each of the genotypes. Seedlings were grown under optimum irrigation and nutrition. When the 4th leaf was fully expanded gas exchange measurement of the 4th leaf was made by the method as in experiment 1. Water application was withheld and drought was allowed to develop. The moisture content of the soil in the pots was monitored as in Experiment 1. Five days after withholding water when the soil moisture potential approached -1.2 MPa measurements were taken again.

Experiment 3 was carried out in 1.5 m^3 lysimeters filled with sand. Seeds were sown with 9cm distance between rows and 7 cm between plants. Three seeds were sown at each position and at the 3rd leaf stage only one plant was retained. There were 8 blocks and 10 plants of each of the 12 genotypes in each block. One non-experimental row of plants was sown on each side of the block. Optimum irrigation and nutrients were supplied. When the first signs of anthesis appeared, irrigation was stopped in 4 of the blocks and the plants in these blocks were allowed to mature using the reserve moisture in the sand. In the other 4 blocks irrigation was continued but without any additional nutrient supply. However, excessive irrigation was avoided to check washing out nutrients from the sand. The moisture potential of the sand in the stressed blocks was monitored by the method as in experiment 1. When the moisture potential of the sand approached -1.2 MPa gas exchange parameters on flag leaf were made by the method as in experiment 1. Yield and yield components were also recorded.

Measurements of net photosynthesis and transpiration rate in the experiments were taken on clear bright days at light intensities from 992 to 1376 mm m^{-2} s^{-1}. WUE was calculated from the data of net photosyntheis and transpiration as follows:-
Water-use-efficiency (WUE) = Net photosynthesis/Transpiration

Results

There were significant differences ($P < 0.05$ or lower) between the genotypes for Pn and WUE under both well-watered and drought stress conditions (Tables 1, 2 and 3). The genotypes were also different for yield and yield components ($P < 0.05$ or

Table 1. Net photosyntheis (Pn, μmol $Co_2 m^{-2} S^{-1}$), reduction (red.) in Pn due to drought, transpiration (E, mmol $m^{-2} S^{-1}$), stomatal conductance (Gs, mol $m^{-2} S^{-1}$), substomatal Co_2 (Ci, μmol mol^{-1}) and water-use-efficiency (WUE, mmol Co_2/mol H_2O) of 8 genotypes at the 5th leaf stage under well-watered and drought stress (Experiment I).

Genotype	Pn		Red.in	E		Gs		Ci		WUE	
	WW	DS	Pn(%)	WW	DS	WW	DS	WW	DS	WW	DS
48 days after sowing (water was with held from the stressed plants on this day)											
(R) Pk 81	15.4	16.1	-4.5	10.9	11.4	0.779	0.763	268.6	267.8	1.4	1.4
(R) Lu26S	13.7	13.5	1.5	10.8	11.0	0.759	0.739	263.7	261.6	1.3	1.2
(S) Pb85	14.3	14.3	0.0	13.6	13.0	0.797	0.809	264.5	262.7	1.1	1.1
(S) Fd83	13.6	13.3	2.2	12.7	12.2	0.784	0.766	265.6	265.1	1.1	1.1
(R) High-ABA6	14.6	15.4	-5.5	11.8	11.9	0.732	0.729	271.0	269.2	1.2	1.3
(R) High-ABA21	15.2	16.1	-5.9	12.0	12.0	0.772	0.763	268.4	266.8	1.3	1.3
(S) Low-ABA6	14.1	13.9	1.4	12.7	12.8	0.804	0.817	269.2	268.9	1.1	1.1
(S) Low-ABA18	13.5	12.6	6.7	11.2	10.9	0.789	0.767	272.5	277.8	1.2	1.2
Mean	14.3	14.4	-0.5	12.0	11.9	0.777	0.770	267.9	267.5	1.2	1.2
Drought (D)	NS			NS		NS		NS		NS	
G x D	NS			NS		NS		NS		NS	
Genotype effects (G)	*			**		*		NS		**	
LSD (0.05)	1.4			1.2		0.039				0.27	
51 days after sowing (mild drought)											
(R) Pk81	16.2	9.3	42.6	11.5	4.1	0.731	0.243	267.6	278.2	1.4	2.3
(R) Lu26S	13.6	8.1	40.4	11.1	6.0	0.719	0.223	263.7	280.1	1.2	1.4
(S) Pb85	14.7	5.1	65.3	13.9	6.0	0.786	0.261	264.0	280.3	1.1	0.9
(S) Fd83	13.1	6.5	50.4	12.8	5.6	0.738	0.310	265.3	286.7	1.0	1.2
(R) High-ABA6	15.6	7.5	51.9	12.1	4.2	0.666	0.246	270.7	275.8	1.3	1.8
(R) High-ABA21	15.7	8.3	47.1	12.2	5.0	0.726	0.211	265.7	279.9	1.3	1.7
(S) Low-ABA6	13.9	6.8	51.1	12.9	5.9	0.796	0.342	270.1	284.8	1.1	1.2
(S) Low-ABA18	12.7	5.2	59.1	11.3	6.1	0.769	0.346	274.1	288.1	1.1	0.9
Mean	14.4	7.1	51.0	12.2	5.4	0.741	0.273	267.7	282.2	1.2	1.4
Drought (D)	**			**		**		**		**	
G x D	**			**		**		NS		**	
Genotype effects (G)	**			**		**		NS		**	
LSD (0.05)	1.7			1.1		0.054				0.22	

Table 1 (Cont'd)

Genotype	Pn		Red.in	E		Gs		Ci		WUE	
	WW	DS	Pn(%)	WW	DS	WW	DS	WW	DS	WW	DS
	53 days after sowing (severe drought)										
(R) Pk81	16.8	4.7	72.0	12.1	3.5	0.714	0.178	270.7	282.4	1.4	1.3
(R) Lu268	14.8	4.2	71.6	11.3	4.3	0.702	0.170	265.3	288.0	1.3	1.0
(S) Pb85	15.7	2.1	86.6	13.7	4.9	0.747	0.196	268.4	289.1	1.2	0.4
(S) Fd83	14.1	2.6	81.6	13.1	4.1	0.718	0.198	268.8	295.8	1.1	0.6
(R) High-ABA6	16.2	4.1	74.7	12.6	3.7	0.683	0.191	271.8	281.7	1.3	1.1
(R) High-ABA21	16.3	4.3	73.6	12.8	4.1	0.708	0.142	269.7	284.0	1.3	1.1
(S) Low-ABA6	14.9	3.5	76.5	13.2	4.5	0.832	0.205	270.9	290.5	1.1	0.8
(S) Low-ABA18	13.2	2.3	82.6	11.7	5.1	0.718	0.215	273.2	300.6	1.1	0.5
Mean	15.3	3.5	77.4	12.6	4.3	0.728	0.187	269.9	289.0	1.2	0.9
Drought (D)	**			**		**		**		**	
G x D	**			**		**		NS		**	
Genotype effects (G)	**			**		**		NS		**	
LSD (0.05) for genotype	1.4			0.9		0.046				0.21	

(R), drought resistant; (S), drought susceptible, (ww) well-watered, (DS) drought stress
*, $P < (0.05)$; **, $P < (0.01)$, NS, not significant.

lower) except for yield under well-watered conditions (Table 4). In experiment 1 plants under well-watered and drought stress treatments were maintained and measured at the same time. The interaction between genotype and drought was significant (51 DAS & 53 DAS, Table 1). In experiment 3 the drought stressed and well-watered blocks were not randomized to avoid seepage from the well-watered blocks to the stressed blocks. In experiment 2 measurements of well-watered and stressed plants were not taken at the same time. Hence the genotype x drought interaction was not calculated in experiments 2 & 3. The effects of genotype for sub-stomatal CO_2 were not significant in any of the experiments both under well-watered and drought conditions. Data for average values of gas exchange measurements in experiment 1 (Table 1), experiment 2 (Table 2) and in experimet 3 are given in Table 3.

The results of experiment 1 revealed that a single measurement only at the severe stress level was sufficient to compare the genotypes for gas exchange response (Table 1). Therefore in the subsequent experiments the genotypes were measured only under well-watered and severe stress conditions. To test if there were systematic variations in light intensity the values recorded for individual genotypes and treatments in the experiments were compared by analysis of variance (data not shown). This showed that there were no significant differences between the genotypes and treatments in mean

Table 2. Net photosyntheis (Pn, μmol $CO_2 m^{-2} S^{-1}$), reduction in Pn under drought, transpiration (E, mmol $m^{-2} S^{-1}$), stomatal conductance (Gs, mol $m^{-2} S^{-1}$), substomatal CO_2 (Ci, μmol mol^{-1}) and water-use-efficiency (WUE, m mol CO_2/mol H_2O) of 12 genotypes at the 4th leaf stage under well-watered and drought stress is experiment 2)

Genotype	Pn		Red.in	E		Gs		Ci		WUE	
	WW	DS	Pn(%)	WW	DS	WW	DS	WW	DS	WW	DS
(R) Pk81	17.3	4.9	71.7	12.3	3.4	0.856	0.162	282.4	288.4	1.4	1.4
(R) Br83	15.7	3.6	77.1	13.4	3.3	0.835	0.168	282.1	295.3	1.2	1.1
(R) Lu26S	14.8	4.4	70.3	11.3	3.7	0.824	0.156	275.3	292.8	1.3	1.2
(S) Pb85	15.3	3.3	78.4	14.7	4.3	0.928	0.188	286.6	295.3	1.0	0.8
(S) Fd85	14.8	2.7	81.8	13.9	4.0	0.863	0.182	277.2	303.6	1.1	0.7
(S) Fd83	14.7	3.9	73.5	13.7	3.7	0.875	0.193	280.7	296.2	1.1	1.1
(R) High-ABA1	16.8	4.7	72.0	13.0	3.5	0.851	0.138	285.4	290.2	1.3	1.3
(R) High-ABA6	15.9	4.1	74.2	13.9	3.3	0.782	0.175	283.8	287.5	1.1	1.2
(R) High-ABA21	16.1	4.8	70.2	13.7	3.6	0.834	0.114	281.3	292.3	1.2	1.3
(S) Low-ABA6	15.2	4.2	72.4	14.4	4.2	0.982	0.203	283.5	296.1	1.1	1.0
(S) Low-ABA18	14.2	3.7	73.9	11.8	4.6	0.923	0.216	291.5	306.5	1.2	0.8
(S) Low-ABA21	13.4	3.1	76.9	14.2	4.4	0.883	0.213	287.3	304.3	0.9	0.7
Mean	15.4	4.0	74.4	13.3	3.8	0.869	0.176	283.0	295.7	1.2	1.1
Genotype effects	**	**		**	**	**	**	NS	NS	**	**
LSD (0.05)	2.1	1.0		1.2	0.8	0.090	0.034			0.12	0.14

(R), drought resistant; (S), drought susceptible, (ww) well-watered, (DS) drought stress

*, P <(0.05); **, P<(0.01), NS, not significant.

light intensity when the measurements were made. Pn and WUE under drought were generally higher for drought resistant genotypes compared to the drought susceptible genotypes both under well-watered and drought stress conditions in all the experiments. Transpiration rate and stomatal conductance were generally lower for the drought resistant genotypes under both the treatments.

Drought affected all gas exchange parameters and WUE in all the experiments (Table 1, 2 & 3). Pn decreased under drought stress in all experiments. Stomatal conductance was also decreased under drought with a parallel reduction in transpiration rate. Average WUE of all the genotypes was increased under mild drought stress in experiment 1 (51 DAS, Table 1) but was decreased under severe drought (53 DAS). A similar decrease in WUE was also observed under drought in experiments 2 & 3.

Table 3. Net photosyntheis (Pn, μmol $CO_2 m^{-2} S^{-1}$), reduction in Pn under drought, transpiration (E, mmol $m^{-2} S^{-1}$), stomatal conductance (Gs, mol $m^{-2} S^{-1}$), substomatal CO_2 (Ci, μmol mol^{-1}) and water-use-efficiency (WUE, m mol CO_2/mol H_2O) of 12 genotypes at flag leaf stage under well-watered and drought stress is experiment 3)

Genotype	Pn		Red.in	E		Gs		Ci		WUE	
	WW	DS	Pn(%)	WW	DS	WW	DS	WW	DS	WW	DS
(R) Pk81	14.4	3.6	75.0	11.1	3.0	0.890	0.168	285.4	289.1	1.3	1.2
(R) Br83	13.2	2.4	81.8	12.2	2.9	0.882	0.174	284.7	295.4	1.1	0.8
(R) Lu26S	12.4	3.3	73.4	10.1	3.8	0.829	0.161	279.2	294.6	1.2	0.9
(S) Pb85	13.1	1.6	87.8	13.7	3.90.976		0.194	283.4295.5		1.0	0.4
(S) Fd85	11.9	0.9	92.4	12.6	3.6	0.893	0.187	288.4	297.6	0.9	0.3
(S) Fd83	12.2	2.0	83.6	12.7	3.3	0.911	0.199	283.6	298.4	1.0	0.6
(R) High-ABA1	14.2	3.4	76.1	11.9	3.0	0.890	0.156	287.8	293.7	1.2	1.1
(R) High-ABA6	13.3	2.6	80.5	12.5	2.7	0.821	0.181	287.6	289.1	1.1	1.0
(R) High-ABA21	13.4	3.5	73.9	12.5	3.2	0.872	0.128	284.5	294.2	1.1	1.1
(S) Low-ABA6	12.4	2.2	82.3	13.3	3.7	0.988	0.203	286.3	2997.2	0.99	0.6
(S) Low-ABA18	11.4	1.9	83.3	10.9	4.0	0.975	0.211	291.7	301.4	1.0	0.5
(S) Low-ABA21	10.5	1.2	88.6	13.2	4.0	0.921	0.213	289.4	303.2	0.8	0.3
Mean	12.7	2.4	81.5	12.2	3.4	0.904	0.181	286.0	295.8	1.1	0.7
Genotype effects	*	**		**	**	**	**	NS	NS	**	**
LSD (0.05)	1.4	1.6		1.2	0.6	0.081	0.032			0.2	0.2

(R), drought resistant; (S), drought susceptible, (ww) well-watered, (DS) drought stress
*, P <(0.05); **, P<(0.01), NS, not significant.

However, the decrease in WUE varied between the genotypes. Drought susceptible genotypes showed a higher decrease in WUE because of their higher reduction in Pn. Sub-stomatal CO_2 increased under drought in all the genotypes. However, the increase was slightly higher for drought susceptible genotypes which showed higher reduction in Pn.

The values of gas exchange parameters of the genotypes were consistent between the experiments under both well-watered and drought stress conditions. There was a significant positive correlation ($r = 0.59$, $P < 0.05$) between grain yield and Pn under drought. Similarly there was a significant positive correlation ($r = 0.69$, $P < 0.01$)

Table 4. Comparison of 12 genotypes for grain yield (g per plant), % yield reduction under drought compared to well-watered conditions, grain per spike, grain weight (g/100 seeds), tillers per plant and plant height (cm) in lysimeters under well-watered (WW) & drought stress (DS) conditions in Experiment 3).

Genotype	Pn		Red.in	E		Gs		Ci		WUE	
	WW	DS	Pn(%)	WW	DS	WW	DS	WW	DS	WW	DS
(R) Pk81	13.5	9.9	26.7	60.1	58.4	3.92	3.12	6.5	6.4	85.2	81.5
(R) Br83	11.8	8.2	30.5	53.8	51.4	3.97	3.15	6.2	5.8	86.4	83.2
(R) Lu26S	13.6	9.6	29.4	48.8	46.3	4.93	3.86	6.8	6.7	92.4	90.1
(S) Pb85	13.7	6.8	50.4	52.4	46.2	3.19	2.14	7.8	7.5	77.3	74.0
(S) Fd85	12.2	7.6	37.7	46.3	41.5	3.81	2.76	7.5	7.2	76.8	73.6
(S) Fd83	11.6	6.9	40.5	44.9	40.3	4.03	2.83	7.2	6.9	71.3	68.1
(R) High-ABA1	10.3	7.9	23.3	50.2	47.8	3.56	2.61	6.8	6.7	72.8	69.6
(R) High-ABA6	12.5	7.8	37.6	58.7	56.2	3.52	2.81	7.2	6.9	67.9	64.3
(R) High-ABA21	10.1	7.7	23.8	52.3	49.2	3.42	2.71	6.8	6.4	72.0	69.3
(S) Low-ABA6	12.6	5.4	57.1	59.4	50.3	3.30	2.26	8.3	6.4	75.7	71.1
(S) Low-ABA18	11.4	5.6	50.9	49.3	42.5	3.48	2.43	7.1	6.5	77.2	74.1
(S) Low-ABA21	10.2	5.5	46.1	53.4	47.6	3.69	2.57	6.7	5.7	81.1	79.2
Mean	12.0	7.4	37.8	52.5	48.1	3.74	2.77	7.1	6.6	78.0	74.8
Genotype effects	NS	**		**	**	**	**	*	*	**	**
LSD (0.05)		1.7		5.4	4.0	0.3	0.3	1.0	0.9	5.1	3.0

(R), drought resistant; (S), drought susceptible, (ww) well-watered, (DS) drought stress

*, $P < (0.05)$; **, $P < (0.01)$, NS, not significant.

between grain yield and WUE under drought. This correlation is based on the average grain yield/plant in experiment 3, and average Pn and WUE values of the same genotypes in experiments 2 & 3. There was a significant positive correlation ($r = 0.96$, $P < 0.01$) between Pn of leaf 4 and flag leaf under drought. There was also a significant positive correlation ($r = 0.97$, $P < 0.01$) between WUE of leaf 4 and flag leaf under drought.

Discussion

The results of the present study support some of the earlier findings that increased stomatal resistance may not have the primary effect on Pn at least under moderate drought stress (Farquar & Sharkey, 1982; Cornic *et al.*, 1983; Krieg & Hutmacher, 1986; Marco *et al.*, 1988). WUE was increased under mild drought but was decreased under severe drought (Table 1, 2 & 3). It implies that transpiration is decreased (as a result of decrease in stomatal conductance) more compared to the decrease in Pn. However, the responses of the genotypes varied. Some drought susceptible genotypes (Pb85 and Low-ABA18) showed decreased WUE even under mild drought whereas, some drought resistant genotypes (Pk81, High-ABA1 and High-ABA21) had higher WUE even under severe drought stress. These results suggest that drought may affect photosynthesis through a direct effect on photosynthetic tissues and that intra-specific genetic variability exists in the genotypes for sensitivity of photosynthetic tissue under drought stress. This variability might be at a thylakoid level. Inherent differences in the sensitivity of the thylakoid membranes to low water potential have been found in earlier studies (Matthew & Boyer, 1984; Quartacci *et al.*, 1995). The differences in Pn between genotypes in the present study under drought can be explained on the basis of an effect on chloroplast activity rather than an effect on CO_2 supply to the mesophyll cells (Farquar & Sharkey, 1982; Peterson, 1985; Castonguay & Markhart, 1992). Higher osmotic adjustment (manuscript in preparation) might have contributed in acclimation of photosynthesis under drought (Downton, 1983).

The results of the present study corroborate the findings of Marco *et al.*, (1988) which suggest that CO_2 supply to mesophyll cells is not a limiting factor in photosynthesis under drought. This suggests that reduced stomatal conductance may not be the only cause in reducing the assimilation rate in drought stressed plants (Redshaw & Meidner, 1972). The drought resistant genotypes in the present study had higher Pn than the susceptible genotypes under drought conditions. However, there were no differences between the genotypes in sub-stomatal CO_2. The drought resistant genotypes had higher Pn inspite of having lower conductance (Table 1, 2 & 3). This shows that the availability of CO_2 to the mesophyll cells was not a factor limiting photosynthesis in the drought susceptible genotypes. Instead the limiting factor was the inability of mesophyll cells to assimilate CO_2. This is also evident from the fact that drought stress increased sub-stomatal CO_2 and the increase was higher in the genotypes with low Pn. Non linear relationships between stomatal conductance and CO_2 assimilation have been found in an earlier study (Farquar & Sharkey, 1982). Similarly Pettigrew & Meredith (1994) have reported differences between genotypes in CO_2 assimilation at the same stomatal conductance.

The significant positive correlation observed between Pn and grain yield under drought stress in the present study corroborate the results of Kaul (1974) which suggest that the relative yield performance of wheat cultivars under drought may be predictable from the Pn of their leaves. In the present studies Pn of 4th and flag leaves under drought stress were correlated. This implies that selection of genotypes for higher Pn can be performed at early seedling stages. Similar results have been found by Krieg & Hutmacher (1986).

WUE of drought resistant genotypes was higher and there was a significant positive correlation between grain yield and WUE under drought in the present study. This supports the earlier results of Blum *et el.*, (1983) and Castonguay & Markhart (1992). The need to increase carbon assimilation without a concomitant increase in transpirational water loss is obvious for most of our current crop species and productive systems (Krieg & Hutmacher, 1986). In wheat, genetic variation in WUE has been attributable to variation in both stomatal conductance and photosynthetic capacity (Condon & Richard, 1993). However, the results of the present study and that of Pettigrew & Meredith (1994) suggest that Pn of genotypes may be different at the same stomatal conductance. So it is possible to select genotypes with increased WUE (Castonguay & Markhart, 1992).

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