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Interactions among Carbon Isotope Discrimination, Water Use Efficiency and Nitrogen Nutrition in Wheat and Barley***

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밀과 보리에 있어서 炭素同位元素差別, 水分利用效率, 窒素營養間의 相互作用***

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ABSTRACT : Large and small seeds (44 and 22 mg per caryopsis) of a spring wheat (cv. Kulin) and a spring barley (cv. Skiff) were sown at two nitrogen rates (equivalent to 10 and 32 g m^{-2}) in well-watered pots under outdoor conditions to determine the effects of seed size and nitrogen (N) nutrition on water use efficiency (WUE) and carbon isotope discrimination (△) and to evaluate interaction among △, WUE and N nutrition in wheat and barley. Barley produced, on average, 105% more biomass (root+shoot dry weight) than wheat at stem elongation because of early vigor. By anthesis this difference had disappeared as wheat had 16% more biomass than barley which headed 3 days earlier. Compared to plants grown from small seed, plants grown from large seed had much greater biomass in wheat than in barley at stem elongation and anthesis. Higher N nutrition increased average biomass of wheat and barley by 40 and 31%, respectively, at anthesis. Barley had 35 and 20% greater WUE (biomass gained/transpiration) than wheat at stem elongation and anthesis, respectively, and 2.0 to 3.6% lower △ in aboveground shoots depending on growth stages and plant parts than wheat which had a greater stomatal conductance than barley. Seed size had a variable effect on WUE and did not affected △ values. Water use efficiency was not affected by N rate at stem elongation in wheat and barley whereas WUE was increased 2 and 7%, respectively, in wheat and barley at anthesis with increasing N from 10 to 32 g m^{-2}. High N plants had about 2.5% lower △ values regardless of growth stages than low N plants across species and seed sizes. Carbon isotope discrimination was negatively correlated with WUE at anthesis but not at stem elongation.

Key words : Wheat, Barley, Seed size, Nitrogen nutrition, Water use efficiency, Carbon isotope discrimination

Greater early growth in winter-sown temperate cereals in Mediterranean environ-

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ments results in a greater WUE because of more growth when it is cool and a reduction in water lost from the soil surface which translate to more water use by the crop. Barley is more vigorous than wheat from the time of emergence. Lopez-Castaneda et al.[29] found that barley produced about 40% more aboveground dry matter and two times greater leaf area by the two-leaf stage. Seedlings grown from large seeds generally accumulate more dry matter than seedlings grown from small seeds in wheat[17,28] and barley[3,25]. Favourable nitrogen nutrition also results in faster early growth and greater accumulation of biomass[2].

Atmospheric carbon dioxide contains approximately 98.9% of the stable isotope ^{12}C and 1.1% of ^{13}C[13]. During photosynthesis, plants discriminate against ^{13}C because of small differences in physical and chemical properties imparted by the difference in mass[33]. The discrimination is particularly large in C_3 species. In C_3 species, △ is caused by the primary carboxylating enzyme, ribulose-1,5-bisphosphate carboxylase which discriminate against ^{13}C and by diffusion from the atmosphere to the site of CO_2 fixation[13]. The discrimination of the diffusive step is 4.4‰ and that of the carboxylation step is about 27.0‰. Farquhar et al.[14] developed a theory that the extent of discrimination against ^{13}C is related to instaneous water use efficiency (WUE) and that △ provides a long-term estimate of the WUE. Farquhar and Richards[15] suggested that △ of plant material in C_3 species is determined by the long-term average ratio of leaf intercelluar (Ci) to atmospheric (Ca) concentrations of CO_2. At constant Ca, the Ci/Ca ratio is determined by Ci which depends on the balance between photosynthetic capacity per unit leaf area and stomatal conductance to CO_2 diffusion. Lower △ is associated with lower Ci. Genotypic variation in △ has been demonstrated in various C_3 species including wheat[1,4,5,9,10,11,32] and barley[7,20]. Because △ provides a simple, integrative assessment of genotypic variation in WUE, △ is receiving increasing attention as a possible selection criterion for improved WUE in various C_3 crops.

Leaves with high N concentration have been found to have both lower leaf Ci and greater instantaneous WUE than leaves with low N concentration when wheat plants were well-watered or grown at high water potentials even though leaves with higher N concentration had a higher stomatal conductance[18,30,31]. These results imply that high level of N nutrition reduces △ values of temperate cereals when water is not limited. Condon et al.[6], however, reported that low N nutrition of container-grown wheat plants, which reduced aboveground dry matter at maturity and leaf area at flag leaf emergence by 30%, had a small but variable effect on △ value.

This study was conducted to determine the effects of seed size and N nutrition on WUE and △ and evaluate the interactions between △, WUE and N nutrition in wheat and barley.

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Materials and Methods

Small and large seeds of a spring wheat (cv. Kulin) and a spring barley (cv. Skiff) were sown at two N rates in pots under natural conditions in Canberra, Australia (147°E, 35°S). Seeds were vernalized for 7 days in the dark at 2℃ and five large or six small seeds per pot were sown at a depth of 2.5 cm on 13 January 1995. Pots were constructed from 15.3 cm inside diameter polyvinylchloride pipe. Each pipe was 50 cm long and was capped at the base. Pots contained a soil mix composed of an equal volume of river sand and river loam. Nitrate and ammonium in the the soil mix were 13.32 and 0.61 ppm, respectively, on a dry weight basis[26)]

Maximum and minimum air temperatures averaged 25.5 and 12.6℃, respectively, and the average daily solar radiation was 18.85 MJ m^{-2} during the experiment.

The mean grain weight of large seeds for wheat was 44 mg (42.6 to 45.4 mg) and that of small seeds was 22 mg (20.6 to 23.4 mg) whereas the barley kernels that had husks averaged 49 mg (47.1 to 50.9 mg) for a large seed and 24.5 mg (23.6 to 25.4 mg) for a small seed. The heavier barley kernels were sown to offset the weight of the husk. The average weight of husk in Skiff was 5 mg for a large seed and 2.5 mg for a small seed.

After sowing the soil surface was covered with about 1 cm of gravel to reduce soil water evaporation and all pots were kept moist. Eight days after sowing (at about the 1.5 leaf stage), all pots were thinned to two healthy seedlings per pot. Pots were also fully irrigated and allowed to drain overnight after which they were weighed. A pot without plants (blank pot) was added to each block to estimate evaporation from the soil surface. The pots were weighed every 3 or 4 days depending on water used and rainfall and amount of water equal to the loss in weight was added. Whenever rainfall was anticipated, transparent plastic rain shelters were placed over the pots.

Phosphorus (equivalent to 15 g m^{-2}) and potassium (15 g m^{-2}) were incorporated in the upper 10 cm of soil at planting as single superphosphate and potassium chloride, respectively. The N rates were equivalent to 10 and 32 g m^{-2} applied as urea in low- and high-N treatments. Half of the urea was applied to each pot at 10 days after sowing and the other half at 17 days after sowing.

A split plot design with three blocks was used. The main-plots consisted of the two species. The subplots consisted of the combination of two seed sizes and two N rates. There were two replicates within each subplot.

Stomatal conductance to water vapor of leaves from plants grown from the large seeds of each species was determined during cloud free periods. Measurements were made on flag, flag-1 and flag-2 leaves between 0910 and 1430 hours on 4 days around anthesis. For each species, 8 measurement were made on both the adaxial and abaxial leaf surfaces using a Delta-T diffusive resistance porometer (Model AP4, Delta-T Devices, Burwell, UK). Total stomatal conductance was obtained by summing the conductance of the adaxial and abaxial surfaces.

One replicate (one pot) of each treatment was harvested at stem elongation (32 days after sowing) and at anthesis (60 days after sowing for wheat and 56 days after sowing for barley). The aboveground shoots were counted and then removed at the soil surface. Green leaves were separated from the shoots to determine leaf area at stem elongation. At anthesis, shoots were separated into green leaves, culm+leaf sheaths +dead leaves, and ears. The leaf area of each plant was measured using an area meter (Model LI-3100, LI-COR, Lincoln, NE) and the number of spikelets per culm was counted. The soil was carefully washed from the belowground shoots and roots, and the roots were separated from the belowground shoots to measure shoot and root biomass. Plant materials were dried at 70℃ for at least 2 days before weighing. Water use efficiency was calculated as grams total biomass (shoots+roots) gained per kilogram water transpired with correction for the water loss due to evaporation from the soil surface.

Nitrogen content and C isotope discrimination of aboveground shoots harvested at stem elongation and both straw and ears harvested at anthesis were determined. The molar ratios of C isotopes in plant material were determined using a ratio mass spectrometer as described by Condon et al.[4] Carbon isotope discrimination of dry matter was calculated according to the formula given by Hubick et al.[22], assuming a value of -8×10^{-3} for an isotopic composition of the air relative to the standard Pee Dee Formation of belemnite.

Results and Discussion

Summary of analysis of variance for traits measured at stem elongation and anthesis are given in Tables 1 and 2, respectively. At stem elongation, there was no significant interaction among treatments for the number of shoots per plant, root to shoot ratio and carbon isotope discrimination (△) in aboveground biomass. Therefore, the main effect of species, seed size and nitrogen (N) rate for these traits is given in Table 4 and the mean values for species×seed size×N rate treatment for the other traits are presented in Table 3. At anthesis, there was a significant species×seed size×N rate interaction for the number of spiklelets and leaf area which are shown in Table 6. The mean values for the two seed size treatments and two N rates for each species for the other traits which have no significant species× seed size ×N rate interaction are presented in Table 5. Because there was no significant species×N rate interaction for the stomatal conductance of the upper three leaves of plants grown from large seeds at anthesis, the main effect of species and N rate is shown in Table 7.

The number of days from sowing to heading was significantly affected by seed size (Table 2). Plants grown from large seed headed 4 days earlier in wheat and 3 days earlier in barley than plants grown from small seed (Table 5). Kaufmann and Guitard[25] also found that development was advanced in spring barley grown from large seed compared to growth from small seed in controlled environment studies.

Barley produced, on average, about 1.4 more shoots per plant at stem elongation (Table 3) and 1.6 more spikes per plant at anthesis than wheat (Table 5). Seed size significantly affected the number of shoots per plant (Table 1) but did not significantly affect the number of spikes per plant (Table 2). There was a significant interaction between species and N rate for the number of spikes since wheat grown at 32 g N m^{-2} had 3.6 more spikes per plant than wheat grown at 10 g N m^{-2} while there was little difference for the number of spikes between two N rates in barley (Tables 2 and 5). The number of spikelets per spike of the two species was increased with increasing N rate except

Table 1. Mean squares from analysis of variance for the number of shoots, leaf area, biomass, root to shoot ratio (R/S), transpiration, water use efficiency (WUE), and N concentration and C isotope discrimination (△) of aboveground shoots of single plants of wheat and barley at stem elongation grown from two seed sizes at two N rates in well-watered pots

Source	df	Shoot number	Leaf area	Root biomass	Shoot biomass	Total biomass	R/S	Transpiration	WUE	N conc.	△
Block	2	3.29	1778	0.017	0.122	0.228	0.0026	26382	0.050	0.067	0.102
Species(S)	1	12.04*	11886*	0.093*	1.737*	2.634*	0.0047	122480*	4.059	0.003	2.261*
Error a	2	0.54	491	0.005	0.047	0.083	0.0010	2413	0.542	0.095	0.072
Seed size (SS)	1	16.67***	12047***	0.138***	1.658***	2.754***	0.0062	199746**	0.481	0.631***	0.292
N rate (N)	1	0.67	939*	0.011	0.000	0.009	0.0098*	298	0.933	3.077***	1.347**
S×SS	1	0.38	2893***	0.000	0.066**	0.072**	0.0029	882	2.349*	1.117***	0.061
S×N	1	1.04	2586***	0.042**	0.179***	0.394***	0.0047	56115***	0.019	1.600***	0.102
SS×N	1	1.50	38	0.007	0.013	0.040	0.0006	11073*	0.279	0.500**	0.004
S×SS×N	1	2.04	416*	0.029*	0.260***	0.463***	0.0005	3255	0.891	0.721***	0.328
Error b	12	0.53	124	0.004	0.007	0.017	0.0018	1366	0.378	0.030	0.143

*, **, *** Significant at the 0.05, 0.01 and 0.001 probability levels, respectively.

for barley grown from small seed (Table 6). Barley grown from small seeds had 13 spikelets per spike at both N rates.

At stem elongation barley had 65% more leaf area per plant than wheat when averaged across seed sizes and N rates (Table 3). This was attributed to the greater early vigor of barley. A plant grown from large seed had 190 and 23% more leaf area in wheat and barley, respectively, than a plant grown from small seed. Leaf area of wheat grown from both large and small seeds was greatly increased with increasing N from 10 to 32 g m^{-2} while that of barley was not significantly affected by N rate (Table 2). At anthesis, wheat grown from large and small seeds had 55 and 12% greater leaf area, respectively, compared with barley (Table 6). Plants grown from large seed had 27% more average leaf area than plants grown from small seed in wheat while there was little difference in average leaf area between two seed size treatments in barley (Table 6). Leaf area of wheat and barley plants grown from both large and small seeds was markedly increased with increasing N rate.

At stem elongation, averaged across the seed sizes and the N rates, barley had 97% more root biomass, 108% more shoot biomass and 105% more total biomass than wheat probably because of early vigor and/or earliness of barley (Table 3). Lopez-Castaneda et al.[29] also reported that barley was more vigorous than wheat at early growth stages. Plants grown from large seed had about four times greater root and shoot biomass in wheat and about 55% more root and shoot biomass in barley than plants grown from small seed. In general, plants derived from heavier seeds produced larger leaves and greater shoot biomass than those from small seed in wheat[17,28] and barley[3,25]. Nitrogen rate did not significantly affect the biomass of wheat and barley grown from small seed while higher N nutrition increased biomass of wheat grown from large seed but decreased that of barley grown from large seed. In contrast to the results at stem elongation, at anthesis, wheat produced 23% more root biomass, 15% more shoot biomass

Table 2. Mean squares from analysis of variance for days from sowing to heading, the number of spikes, the number of the spikelets per spike, leaf area, biomass, root to shoot ratio (R/S), transpiration, water use efficiency (WUE), and N concentration and C isotope discrimination (△) of straws and ears of single plants of wheat and barley at anthesis grown from two seed sizes at two N rates in well-watered pots

Source	df	Days to heading	No. of spikes	No. of spikelets	Leaf area	Root biomass	Shoot biomass	Total biomass
Block	2	15.1	1.63	0.72	0.3[a]	42[b]	4.9	5.0
Species (S)	1	23.7	7.72	3.00	32.6*	249	10.6	14.1
Error a	2	10.0	0.94	1.22	2.0	28	0.5	0.8
Seed size (SS)	1	61.5**	0.13	0.10	0.6	140*	31.0***	35.3***
N rate (N)	1	4.9	26.18***	5.91***	109.3***	549***	33.4***	42.5***
S×SS	1	0.0	0.60	0.78	6.4*	205*	12.1**	26.5**
S×N	1	0.4	6.80*	0.99	7.5**	182*	4.8	3.1
SS×N	1	13.2	0.60	0.02	15.7***	0	0.9	0.8
S×SS×N	1	0.6	0.19	3.13**	4.2*	8	7.1	7.6
Error b	12	5.8	1.21	0.30	0.7	23	1.5	1.7

Source	df	R/S	Transpi-ration	WUE	N concentration		△	
					Straw	Ear	Straw	Ear
Block	2	1.79[b]	0.07	179[b]	202[b]	3[b]	139[b]	78[b]
Species (S)	1	1.23	2.56*	2805***	34	70**	2503*	778*
Error a	2	0.10	0.01	16	48	0	95	18
Seed size (SS)	1	1.48*	1.74**	11	949***	137*	86	337
N rate (N)	1	0.19	1.53**	125*	9179***	1200***	1357*	1087*
S×SS	1	0.57	1.53**	466***	789***	38	40	213
S×N	1	7.95***	0.70*	44*	464**	55	0	9
SS×N	1	0.05	0.13	30	3	13	151	26
S×SS×N	1	0.06	0.19	2	45	10	0	11
Error b	12	0.26	0.10	16	28	15	157	147

*, **, *** Significant at the 0.05, 0.01 and 0.001 probability levels, respectively.

[a] Reported values must be multiplied by 10^3.

[b] Reported values must be multiplied by 10^{-3}.

Table 3. Leaf area, biomass, transpiration, water use efficiency (WUE) and N concentration of aboveground shoots of single plants of wheat (W) and barley (B) at stem elongation grown from two seed sizes at two N rates in well-watered pots

Seed size	N rate	Leaf area		Root biomass		Shoot biomass		Total biomass		Transpiration		WUE[a]		N conc.	
		W	B	W	B	W	B	W	B	W	B	W	B	W	B
		······cm²····		······························ g		······························						···g/kg···		···%···	
Large															
	10	82	134	0.17	0.44	0.64	1.46	0.81	1.90	319	594	2.47	3.11	4.59	3.32
	32	121	115	0.24	0.21	0.98	1.04	1.23	1.25	389	424	3.09	2.85	4.73	5.19
	Mean	102	124	0.21	0.33	0.81	1.25	1.02	1.57	354	509	2.78	2.98	4.67	4.26
Small															
	10	21	100	0.05	0.19	0.17	0.78	0.22	0.97	129	334	1.74	2.85	4.43	4.71
	32	49	103	0.05	0.17	0.19	0.87	0.25	1.04	239	296	2.02	3.79	4.69	5.31
	Mean	35	102	0.05	0.18	0.18	0.83	0.24	1.01	184	315	1.88	3.32	4.56	5.01
LSD(0.05)[b]		20		0.11		0.14		0.23		66		1.09		0.31	

[a] WUE=total biomass change/transpiration.

[b] LSD for seed size×N rate interaction within a species.

and 16% more total biomass than barley (Table 5). This greater growth of wheat than barley after stem elongation was attributed to the longer duration to anthesis of wheat than barley. Wheat grown from large seed had 37% more root biomass and 70% more shoot biomass than wheat grown from small seed whereas barley grown from large seed produced only 9% more shoot biomass without increased root biomass compared with barley grown from small seed. A higher N application increased total biomass of wheat and barley by 40 and 31%, respectively, and markedly increased biomass of wheat grown from large seed and that of barley grown from small seed, resulting in a strong species×seed size×N rate interaction for shoot and total biomass. Root to shoot ratio was not affected by seed size but was markedly reduced at the higher N level in the two species at stem elongation (Tables 1 and 4). At anthesis plants grown from large seed had a lower root to shoot ratio than plants grown from small seeds (Table 5). Significant species×N rate interaction was found for root to shoot ratio at anthesis because root to shoot ratio was greater at the low N treatment in wheat but was greater at the

Table 4. The number of shoots per plant, root to shoot ratio, and C isotope discrimination (△) of wheat and barley at stem elongation grown from two seed sizes at two N rates in well-watered pots

Treatment	No. of shoots	R/S	△
Species	‰	‰	‰
Wheat	3.6***	0.263	19.3**
Barley	5.0	0.235	18.7
Seed size			
Large	5.2***	0.252	19.1
Small	3.5	0.246	18.9
N rate(g/m²)			
10	4.2	0.269*	19.3**
32	4.5	0.229	18.8

*, **, *** Significant differences between the means of two treatments within species, seed size, or N rate at the 0.05, 0.01 and 0.001 probability levels, respectively.

Table 5. The number of days from sowing to heading, the number of spikes, biomass, root to shoot ratio (R / S), transpriration, water use efficiency (WUE) and N concentration and C isotope discrimination (△) of straws and ears of single plants of wheat (W) and barley (B) at anthesis grown from two seed sizes at two N rates in well-watered pots

Treatment	Days to heading		No. of spikes		Root biomass		Shoot biomass		Total biomass		R / S	
	W	B	W	B	W	B	W	B	W	B	W	B
					……… g ………							
Seed size												
Large	49	47	7.1	8.0	1.23	0.87	10.54	7.59	11.77	8.47	0.122	0.115
Small	53	50	6.1	8.3	0.90	0.88	6.18	6.97	7.08	7.85	0.148	1.124
N rate(g / m^2)												
10	51	48	5.0	7.6	1.03	0.63	6.88	6.43	7.91	7.06	0.513	0.999
32	51	49	8.6	8.8	1.12	1.12	9.95	8.13	11.07	9.25	0.119	0.140
LSD(0.05)[a]	3		1.4		0.19		1.53		1.65		0.020	

Treatment	Transpiration		WUE[b]		N concentration				△			
					Straw		Ear		Straw		Ear	
	W	B	W	B	W	B	W	B	W	B	W	B
	……… kg ………		……… g / kg ………		……… % ………				……… ‰ ………			
Seed size												
Large	3.07	1.97	3.82	4.28	1.27	1.74	1.71	1.91	19.4	18.8	17.8	17.6
Small	2.00	1.88	3.54	4.59	2.16	1.73	1.98	1.96	1.94	18.6	17.8	17.2
N rate(g / m^2)												
10	2.15	1.82	3.66	4.26	1.13	0.98	1.63	1.66	19.7	19.0	18.0	17.7
32	2.95	2.04	3.72	4.55	2.13	2.50	2.00	2.21	19.2	18.5	17.6	17.2
LSD(0.05)[a]	0.40		0.16		0.21		0.15		0.5		0.5	

[a] LSD for two means of a treatment within a species.

[b] WUE=total biomass change / transpiration

Table 6. The number of spikelets per spike and leaf area of single plants of wheat and barley at anthesis grown from two seed sizes at two N rates in well-watered pots

Seed size	N rate	No. of spikelets		Leaf area	
		Wheat	Barley	Wheat	Barley
	g/m^2			…cm^2…	
Large					
	10	12.1	12.2	184	130
	32	12.8	13.4	433	267
	mean	12.5	12.8	309	199
Small					
	10	10.3	13.0	205	177
	32	12.9	13.0	284	256
	mean	11.6	13.0	244	217
LSD(0.05)		1.0		47	

[a] LSD for seed size×N rate interaction within a species.

high N treatment in barley which had greater root biomass at the high N treatment. Nitrogen fertilizer generally stimulated shoot growth more than root growth and decreased root to shoot ratio[2,8,27].

There was a strong correlation between total transpiration and total biomass in wheat and in barley at stem elongation and anthesis (Table 8). Strong associations between total water use and biomass have been reported in cowpea[23]. A close linear relationship might imply a constant WUE. However, this was not the case. Despite their strong associations, significant species and N rate effects on WUE were observed at anthesis (Table 2). By stem elongation, wheat had transpired 35% less water and produced 51% less total biomass than barley across seed sizes and N rates, resulting in 26% less WUE in wheat than in barley. There was a significant species×seed size interaction for WUE at stem elongation because wheat grown from large seeds had 48% greater WUE than wheat grown from small seeds whereas WUE of barley grown from small and large seeds were similar (Table 3). The lower WUE of wheat may partly be due to the greater loss of water from the soil surface from the smaller plants. Nitrogen rate did not significantly influence WUE at stem elongation. At anthesis, averaged across seed sizes and N rates, wheat transpired 34% more water but had 18% more total biomass than barley. Therefore, wheat had 17% lower WUE than barley. Lower WUE of wheat was probably due to higher leaf stomatal conductance of wheat compared with barley (Table 7). Wheat had greater stomatal conductance

Table 7. Stomatal conductance of upper three leaves at anthesis in wheat and barley grown from large seed at two N rates in well-watered pots

Treatment	Flag leaf			Penultimate leaf			Flag-2 leaf		
	Adaxial	Abaxial	Total	Adaxial	Abaxial	Total	Adaxial	Abaxial	Total
	…………	…………	…………	…………	$mmol\ m^{-2}\ s^{-1}$	…………	…………	…………	…………
Species									
Wheat	449^{**}	299	747^{**}	405^{*}	245	650	282	172	453
Barley	212	298	510	220	300	520	172	212	383
N rate									
10	324	293	617	266^{*}	241^{+}	507^{*}	161^{**}	139^{**}	299^{**}
32	337	303	640	359	304	663	293	245	537

$^{+}$, *, ** Significant differences between the means of two treatments within species, or N rate at the 0.10, 0.05, and 0.01 probability levels, respectively.

of adaxial surface of flag and penultimate leaves than barley. Significant species×seed size and species×N rate interactions were observed for WUE at anthesis. Plant grown from large seed, on average, had 8% greater WUE in wheat but 7% less WUE in barley. Higher N nutrition significantly increased WUE of barley but not that of wheat averaged across seed sizes. Morgan[30,31] also reported that instantaneous WUE, calculated as CO_2 exchange rate/transpiration, was greater in high N wheat than in low N wheat. Nitrogen application has been known to increase WUE of various crops under field conditions[35].

In this study △ was significantly influenced by species and N rate both at stem elongation and at anthesis (Table 1 and 2). On average, △ in aboveground dry matter was 2.0 to 3.7% higher in wheat than in barley depending on plant parts and growth stages (Tables 4 and 5). Greater △ values in wheat than barley could be due to the greater stomatal conductance in wheat compared to barley. Substantial genotypic variation in △ within a species has been reported in wheat[1,4,5,9,10,11,32], barley[7,20] and some other C_3 species[21,22,24,34,36]. As described in the Introduction, △ depends on the balance between photosynthetic capacity and stomatal conductance. Lower values of △ may result from lower stomatal conductances and/or greater photosynthetic capacity. In common bean, genotypic variation in △ seems to principally arise as a result of variation in stomatal conductance[12]. By contrast, in peanut much of the genotypic variation in △ appears to be due to variation in photosynthetic capacity[22]. In wheat, variation in stomatal conductance and in photosynthetic capacity contributes equally to genotypic variation in △[5]. Averaged across species and seed sizes, high N plants had about 2.5% lower △ in aboveground shoots at stem elongation and anthesis compared with low N plants (Tables 4 and 5). This indicates that the photosynthetic capacity of high N plants increased more than stomatal conductance in both wheat and barley. The high N plants also had greater stomatal conductance of penultimate (flag-1) and flag-2 leaves. Plants with more N also had higher N concentration of aboveground

Table 8. Simple correlation matrix for total biomass, transpiration, water use efficiency (WUE), and C isotope discrimination (△) of single plants of wheat and barley grown from large seed at two N rates in well-watered pots

	Total biomass			Transpiration			WUE		
	Wheat	Barley	Pooled	Wheat	Barley	Pooled	Wheat	Barley	Pooled
					At stem elongation				
Trans.	0.890**	0.937**	0.933***						
WUE	0.826**	−0.03	0.578**	0.686*	−0.360	0.330			
Shoot △	0.142	0.03	−0.305	0.137	0.157	0.200	0.148	−0.298	−0.374^{+}
					At anthesis				
Trans.	0.966***	0.936***	0.944***						
WUE	0.782**	0.341	0.067	0.726*	−0.006	−0.259			
Shoot △	−0.462	0.090	0.063	−0.485	0.077	0.169	−0.577^{+}	−0.612*	−0.729**
Ear △	*−0.444*	*0.100*	*0.003*	−0.462	0.279	0.118	−0.615*	−0.601^{+}	−0.588**

$^{+,*,**,***}$ Significant at the 0.10, 0.05, 0.01 and 0.001 probability levels, respectively.

shoots than low N plants in the two species (Table 5). Higher N nutrition has been reported to increase stomatal conductance and photosynthesis in wheat when water was not limited[16,18,30,31]. Condon et al.[6] reported that even though a variable effect of N nutrition on △ was found at flag leaf emergence, grain △ was lower at high N treatment in wheat. However, in peanut △ was not affected by the N treatment[19].

As predicted by the theory[14], a negative relationship between △ and WUE associated with different genotypes has been reported for a number of C_3 species including wheat[1,4,5,9,10,11,32] and barley[7,20]. Therefore, △ has been proposed as a selection criterion for improving the WUE of C_3 species. In this study △ in aboveground shoots of plants differeing in seed size and N nutrition was not correlated with WUE of the two species at stem elongation but a negative correlation between the two traits was observed in the two species at anthesis (Table 8). Carbon isotope discrimination was not significantly associated with total biomass in either species at stem elongation nor at anthesis (Table 8). The principal reason for this finding at anthesis was the different harvest times of wheat and barley.

Fast early vigour has been proposed as an important trait to improve the growth and WUE of crops grown in Mediterranean type environments where terminal drought is normal. This was evident here. By the time of stem elongation the treatment combining high vigour traits (large seed, high N, barley) produced five times more biomass than the low vigour treatment (small seed, low N, wheat). Water use efficiency was also 65% greater in the high vigour treatment. Although some of these differences had disappeared by anthesis under the very favourable conditions of this experiment, large seeded treatments had 35% more biomass than small seeded treatments. The large difference in biomass between the high and low vigour treatments may be maintained if conditions were less favourable and there was a terminal drought. However, the effect of seed size on biomass may be minimized in winter wheat and barley because the period of vegetative development is longer in winter wheat and barley than in spring wheat and barley.

Because early vigor and proper N application result in more growth when it is cool and reduce water lost from the soil surface, and increase the amount of water available for transpiration, sowing optimum maturing cultivars with early vigor and with large seed and application of proper N to temperate cereals could be the best practices for improving crop WUE in water-limited Mediterranean-type environments where terminal drought is normal. Additional advantages of early vigor and proper N nutrition are reduction of weed populations and herbicide use regardless of water availability.

摘 要

밀과 보리에 있어서 종자크기와 窒素營養이 水分利用效率과 炭素同位元素差別에 미치는 영향을 조사하여 炭素同位元素差別, 水分利用效率, 窒素營養間의 상호작용를 구명하고저 종자크기가 穎果當 각각 44mg과 22mg인 춘파형 밀과 보리 한 품종을 직경이 15.3cm인 폿트에서 2본씩 재식, m^2당 窒素 10g과 32g 비율로 시용하여 水分利用效率에 관련된 형질과 炭素同位元素差別을 조사하였다.

두 종자크기와 두 질소 시비량을 평균한 乾物重

은 節間伸長期에는 보리가 밀보다 105% 컸던 반면 開花期에는 보리보다 출수가 3일 늦은 밀이 보리보다 16% 많았다. 節間伸長期과 開花期에 있어서 보리에 비하여 밀에서 乾物重에 미치는 대립종자의 영향이 컸었다. 다질소구가 소질소구에 비하여 開花期에 있어서 밀과 보리의 건물중이 각각 40%와 31% 높았다. 節間伸長期와 開花期에 있어서 水分利用效率은 보리가 밀보다 각각 35%와 20% 많았고, 지상부의 炭素同位元素差別은 밀보다 보리가 생육기와 식물체 부위에 따라 2.0~3.6% 적었다. 종자크기가 水分利用效率에 미치는 영향은 뚜렷한 경향이 없었고 炭素同位元素差別에도 유의한 영향을 주지 않았다. 節間伸長期에 있어서 水分利用效率은 질소영양에 의하여 영향을 받지 않았으나 開花期에 있어서는 소질소구에 비하여 다질소구에서 밀과 보리가 각각 2%와 7% 컸었다. 두 맥종과 두 종자크기를 평균한 炭素同位元素差別은 생육시기에 관계없이 다질소구에서 소질소구보다 약 2.5% 낮았다. 炭素同位元素差別은 절간신장기에는 水分利用效率과 유의한 상관관계가 없었으나 開花期에 있어서는 負의 상관이 있었다.

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