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EFFECT OF GENOTYPE VARIABILITY ON NITRATE UPTAKE AND ASSIMILATION OF BARLEY CULTIVARS

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ABSTRACT

Nitrate concentration in the soil at the start of the growing season is high because of mineralization of organic N during autumn and the addition of N fertilizer. It may be useful to exploit this N as much as possible. Therefore, nitrate uptake, assimilation and dry matter production among a range of barley cultivars were examined in a series of experiments utilizing a hydroponic system. Seedlings were grown at two rates of nitrates, i.e., 0 and 1.0 mM and the experiments lasted for 20 or 26 d. Significant genetic differences in growth and nitrate uptake were identified. The cultivars 'Skiff' and 'Franklin' consistently produced large seedlings which took up large quantities of nitrate from solution whereas 'Stirling', 'Schooner' and 'Triumph' produced small seedling and took up small amounts of nitrate. However, apart from differences based on seedling vigor, there was evidence that a group of cultivars which had the Victorian cultivar Research as a common parent was more efficient physiologically in assimilating nitrate. For comparable amounts of nitrate taken up from solution, total dry matter production in this group of cultivars was consistently greater than the other cultivars examined. Results from this work established that genetic differences in nitrate uptake exist between cultivars which in most cases were related to the size of the plant, especially the root system. However, the importance of greater nitrate uptake by the seedling and consequently of early growth, to grain yield was not clearly established because early vigor was not always early beneficial to yield.

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KEY WORDS: Barley, Genetic variability, *Hordeum vulgare*, Nitrate assimilation, Nitrate uptake.

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اثر تنوع ژنوتیپی بر جذب و استفاده نیترات در ارقام مختلف جو

قدرت اله فتحی و جی. ک. مک دونالد

به ترتیب دانشجوی سابق دوره دکترا (اکنون استادیار مجتمع عالی آموزشی و پژوهشی کشاورزی رامین، دانشگاه شهید چمران اهواز، جمهوری اسلامی ایران) و استاد بخش علوم گیاهی، دانشگاه آدلاید، استرالیا.

چکیده

درشروع فصل رشد میزان غلظت نیترات در خاک زیاد است، زیرا معدنی شدن ازت آلی در طول فصل پاییز انجام شده است، و از طرفی معمولاً کود ازته شیمیایی نیز به خاک اضافه می شود. لذا استفاده هر چه بهتر از این مقدار ازت در خاک بسیار سودمند خواهد بود. در این آزمایش، تفاوت های ژنتیکی جذب و استفاده نیترات و همبستگی آن با تولید ماده خشک چند رقم جو با روش آبکشت ، بررسی شد. گیاهچه ها در دو غلظت نیترات (صفر و ۱ میلی مولار) و در دومرحله رشد ۲۰ روزه و ۲۶ روزه با هم مقایسه شدند. نتایج بررسی نشان داد که اختلاف معنی داری از نظر رشد و میزان جذب نیترات میان ارقام مختلف وجود داشت. ارقام 'Skiff' و 'Franklin' که نیترات بیشتری را جذب کردند تولید گیاهچه بزرگتری نمودند، در حالی که ارقام 'Schooner'، 'Stirling' و 'Triumph' که مقدار کمتری نیترات را جذب کرده بودند گیاهچه کوچکتری بوجودآوردند. بر اساس تفاوت ارقام از نظرتوان گیاهچه، نتایج نشان داد که گروه ارقامی که پس از بررسی های انجام شده در ایالت ویکتوریا انتخاب گردیدند دارای کارایی فیزیولوژیکی بیشتری در استفاده از نیترات بودند. میزان ماده خشک تولید شده توسط این ارقام با توجه به میزان نیترات جذب شده بیشتر بود. نتایج این مطالعه بیانگر این است که تفاوت های ژنتیکی در جذب نیترات بین ارقام مختلف جو در بیشتر موارد در ارتباط با اندازه گیاه و بطور خاص سیستم ریشه است. همچنین، جذب بیشتر نیترات بوسیله گیاهچه و رشد اولیه مطلوب، همواره باعث افزایش عملکرد دانه نخواهد شد.

INTRODUCTION

Nitrate and ammonium are the most important forms of N utilized by cereals although urea is also supplied to plants as fertilizer. Nitrate, however, is the most common form of N taken up by cereal plants growing in the field, and efficient utilization of soil and fertilizer N is an important and desirable agronomic character in barley. Under most soil conditions ammonium fertilizer is rapidly nitrified to nitrate by soil organisms (3, 9, 10). Early in the season, nitrate in the soil tends to be high and so it would be desirable to use as much of this nitrate as possible. There are clear indications that active ion absorption by plants is under genetic control (3, 6) and that considerable differences exist between varieties. The variation is due to differences in the size and morphology of the roots, demand for mineral elements caused by differences in relative growth rate (2, 12, 14), uptake and transport (6, 7) and use efficiency. The present study represents an attempt to evaluate the level of genetic variation in nitrate uptake and assimilation in barley at the seedling stage.

Fathi *et al.* (5) on the basis of differences in nitrate uptake and dry matter accumulation, categorized different cultivars into two main groups. 'Stirling' and 'Schooner' were small plants, which took up less nitrate but had higher relative growth rates than the semi-dwarf cultivars, 'Skiff' and 'Franklin'. It was thought that these differences could be related to the pedigrees of the cultivars. Therefore, the preliminary experiments were extended to look at a greater number of cultivars representing four genetic groups. The aim of the present study was to verify the differences in the response of the barley cultivars to nitrate in order to extend the results by looking at nitrate uptake and dry matter production in a larger number of cultivars. The cultivars chosen represented four groups each with a common or similar genetic background.

MATERIALS AND METHODS

The study was conducted as three separate experiments because there was insufficient space in the growth room to do all the comparisons at the same time. In each experiment the semidwarf group was compared with one of the other groups.

Plant Material

Nineteen improved cultivars of barley were obtained from the collection of the Waite barley breeding program (Table 1). Each cultivar is a commercial variety or advanced breeding line. The cultivars were

Table 1. Pedigree of barley cultivars used for the study of nitrate uptake.

Cultivars	Pedigree
Group I	(SD and 'Shannon' group)†
'Skiff'	((AD×WI-2335)×(CD 28×WI-2231))/165
'Franklin'	'Shannon' ×'Triumph'
'Triumph'	(HADM.24566×Diamant×1402/64)(ALSA×Abyssinian×St. ×Union)
'Shannon'	Proctor* 4/Ethiopian line Cl-3208-1
'WI-2869'	('Triumph'* 'Galleon')/77a
Group II (T)[§]	
'Stirling'	'Dampier'//(A14)Prior/Ymer/3/Piroline
'Dampier'	Olli selection (M98)/Research
'Forrest'	Atlas 57/(A16) Prior/Ymer
'Grimmett'	Bussel/Zephyr
'WI-2966'	('Schooner' * Forrest)/55
Group III (T)	"Prior/Proctorgroup"
'Schooner'	Proctor/PriorA//Proctor/Cl-3576
'Clipper'	Proctor/PriorA
'Galleon'	'Clipper'/Hiproly//3* Proctor/C1 3576
'Chebec'	(O/Martin* 'Clipper' (2)* WI-2468)-88/5/6/2
'Prior A'	Selected Chevalier
Group IV (T)	"Research group"
'Weeah'	Prior/Research
'Parwan'	Plumage Archer/Prior//Lenta/3/Research/Lenta
'Lara'	Research/Lenta
'WI-2728'	(WI-2468LHR×'Weeah')/7

† 'Shannon' mostly derived from semi-dwarf cultivars. § T=Tall.

classified into four groups, each with a similar or common pedigree:

(i) Group I: Cultivars derived from semidwarf parents, with high nitrate uptake characteristics. 'Skiff' and 'Franklin' were assigned as the leading cultivars.

(ii) Group II: Cultivars which are mostly derived from Western Australian cultivars and crosses involved Western Australian cultivars. The leading cultivar of this group, 'Stirling', has been found to have low nitrate uptake characteristics in the early stages of growth. 'Grimmett' is a Queensland cultivar.

(iii) Group III: These cultivars have been derived either from 'Prior A'(originally from England) or 'Clipper'(a derivative of 'Prior A'). 'Schooner', the leading cultivar in this group has low nitrate uptake characteristics.

(iv) Group IV: This group consisted mainly of Victorian cultivars, with the variety Research as a common parent. The leading cultivar 'Weeah' has been recognized as having high nitrate uptake characteristics.

In Experiment 1, Groups I and II, in Experiment 2, Groups I and III, and in Experiment 3, Groups I and IV were compared. 'WI-2869' from Group I was used only in Experiment 1.

Growth Conditions

Seeds were sterilized by immersion in 70% ethanol for 1 min, soaked for 5 min in 1% sodium hypochlorite (8 ml 100^{-1} ml de-ionized water) and thoroughly rinsed with deionized water. The seeds were then sown in square plastic pots containing sterilized sand and watered with de-ionized water in a growth room set at 20±4 °C, and a 12 hr photoperiod. Fluorescent and incandescent lamps provided an irradiance of 200-300 μEinstein m^{-1} s^{-1}.

Eight days after emergence the seedlings were removed from the sand and transferred to 6 L round plastic pots with plastic lids. Each lid had 25 holes. Seedlings were supported by inserting their roots through holes in the base of eppendorf tubes, (7 ml capacity) which were placed in the holes in the lid. Twenty four seedling were placed in each pot and grown using a hydroponic system with a 1 mM nitrate solution (Table 2) for 26 d (Experiments 1, 2) or 20 d (Experiment 3) at a pH of 6.0. The remaining hole was used for the supply of air. The aeration rate was 0.9 l min^{-1} for each pot. The nutrient solution in each pot was renewed at 10, 15 and 19 d after seedling transfer. At day 20, the plants were transferred to a nitrate-free solution (Table 2) for 24 hr after which 12 plants in each pot were harvested (H_1). The remaining plants were transferred to a 1 mM nitrate solution for 6 d during which time the solutions were changed every 48 hr. At day 26 (H_2) the remaining 12 plants were harvested and partitioned into root and shoot and their dry weights measured. The experimental design was a randomized complete block with 5 (Experiment 1) and 4 (Experiments 2 and 3) replicates, respectively.

Table 2. Compositions of solutions used for hydroponic studies of nitrate uptake and assimilation.

	Nitrate solutions	
	0.0 mM	1.0 mM
	($mg\ l^{-1}$)	
KNO_3	-	34.1
$Ca(NO3)_2.4H_2O$	-	79.9
$MgSO_4.7H_2O$	7.6	7.6
KH_2PO_4	10.2	10.2
K_2SO_4	218.0	189.4
$CaSO_4.2H_2O$	430.5	372.7
Trace Elements (TE)†	0.36	0.36
Fe-EDTA	21.8	21.8

† TE: ($MnSO_4.7H_2O$ 28 mg l^{-1}, $Na_2MoO_4.2H_2O$ 6 mg l^{-1}, $CaSO_4.5H_2O$ 14 mg l^{-1}, NaCl 145 mg l^{-1}, $ZnSO_4.7H_2O$ 18 mg l^{-1}, $CuSO_4$. $5H_2O$ 31 mg l^{-1}, H_3BO_3 116 mg l^{-1}).

Measurements

The nitrate concentration of the nutrient solution was measured each-time solutions were renewed before first harvest (H_1), and between H_1, and the final harvest (H_2). The absorbance of this solution was measured in a spectrophotometer (model Lambda 5) at 210 nm (1). Nitrate concentrations in the plant parts at H_1 and H_2 were measured as unreduced nitrate by the *E. coli* method (11). Relative growth rate (RGR), nitrate assimilation, nitrate assimilation efficiency (NAE) and nitrate uptake efficiency (NUE) were determined. Growth rate was calculated from the increase in total dry weight during 6 d.

Data Analysis

Analysis of variance was conducted for each experiment on all data parameters. Linear regressions were calculated for relationships between (a) the increase in nitrate between H_1 and H_2 day period and the increase in dry weight over the same time, and (b) the total nitrate uptake over 26 d and total dry weight at H_2. To compare the response of different groups of cultivar, the slopes and intercepts of the regressions were compared using Genstat 5.

Definition of Units

Plants were partitioned into shoot and root after harvest, dried at 80°C for 2 d and the dry weights measured.

(i) The relative growth rate was calculated as: $RGR = (InW_2 - InW_1)/(t_2 - t_1)$, where W_1 and W_2 are total plant dry weights at t_1 and t_2.

(ii) Nitrate accumulation was calculated from the difference between nitrate content in root and shoot at H_1 and H_2. Nitrate concentration of the root and shoot was measured as unreduced nitrate by the *E. coli* method (11).

(iii) Nitrate assimilation was estimated by subtracting the nitrate accumulation in both shoot and root from total nitrate taken up by the plants during the 34 hr.

RESULTS

The inclusion of the Group I cultivars in each experiment allows a comparison to be made between the 3 experiments. The growth and nitrate uptake of the semidwarfs were similar in the first two experiments, but in the third it was a little lower. A possible reason is that the duration of Experiment 3 was 2 d shorter than Experiments 1 and 2. The general consistency in nitrate uptake and growth of semidwarf cultivars in these experiments allow the results of the experiments to be compared.

Experiment 1

There were significant differences in root and shoot growth among the cultivars which were not related to their cultivar groupings (Table 3).'Shannon' and 'WI-2869' (Group I) and 'WI-2966' and 'Forrest' (Group II) produced significantly more root growth than the other cultivars at both harvests. A similar difference, although not as large, was observed also with shoot growth. 'Stirling' had the greatest RGR and the smallest plants. The growth rates of the 10 cultivars were not significantly different from one another, however, there were differences in the RGR. 'Shannon' is not a semidwarf but had quite a different RGR. There were significant differences between cultivars both in the total amount of nitrate taken up over the 6 d and in the nitrate which accumulated in the plant tissue (Table 4).

Table 3. Effect of 1 mM nitrate supplied hydroponically on root, shoot and total dry matter production and growth rate of ten cultivars of barley in Experiment 1.

Cultivar	Root DW (mg plant^{-1})		Shoot DW (mg plant^{-1})		Total DW (mg plant^{-1})		RGR§ (mg plant^{-1})	GR§ (mg plant^{-1})
	H_1†	H_2	H_1	H_2	H_1	H_2		
Group I								
'Skiff'	61	113	176	400	237	513	13.25	46
'Triumph'	66	113	168	419	234	532	13.17	50
'Shannon'	86	142	222	447	308	588	10.77	47
'WI-2869'	74	137	188	480	262	618	14.32	59
Group II								
'Stirling'	38	95	106	311	144	406	17.37	44
'Dampier'	47	94	163	407	210	501	14.35	48
'Forrest'	83	163	230	464	313	627	11.57	52
'Grimmett'	70	114	196	370	266	484	9.93	36
'WI-2966'	78	166	225	513	303	679	13.52	63
LSD(5%)	17	24	39	80	53	96	3.92	NS

† H_1=Harvest 1, H_2=Harvest 2, RGR=Relative growth rate, GR=growth rate.

§ Based on total dry weight.

Table 4. Total nitrate content, increase in nitrate uptake, nitrate uptake per root dry weight, and indices of N use efficiency of 10 cultivars of barley grown with 1mM nitrate in Experiment 1.

	Total NO_3- uptake (μmol plant^{-1}) (0-26 d)	NO_3-uptake† (μmol plant^{-1}) (20-26 d)	Nitrate uptake (μmol root DW^{-1} d^{-1}) (20-26 d)	$\Delta DM/\Delta NO_3$-§ uptake (20-26 d)	Total NO_3- uptake (0-26 d)
Group 1					
'Skiff'	1837	955	3699	0.300	0.285
'Franklin'	1811	937	4003	0.306	0.283
'Triumph'	1759	845	3117	0.337	0.299
'Shannon'	2234	1184	3461	0.233	0.263
'WI-2869'	2169	1180	3695	0.306	0.286
Group 11					
'Stirling'	1451	828	4101	0.346	0.283
'Dampier'	1660	858	4023	0.339	0.305
'Forrest'	2247	1203	3339	0.264	0.279
'Grimmett'	1919	953	3466	0.230	0.252
'WI-2966'	2451	1375	3774	0.274	0.277
LSD(5%)	286	216	NS	NS	NS

† Increase in nitrate uptake over the 6 d.

§ Increase in dry matter over increase in nitrate uptake over the 6 d.

However, as with the dry matter and growth rate data, there was no clear distinction between the two groups. There was no significant difference between cultivars in Groups I and II in nitrate uptake per g root dry weight

(Table 4). Total nitrate uptake per plant did not differ significantly between 'Shannon' and cultivars 'WI-2869', 'WI-2966' and 'Forrest' but 'Shannon', 'WI-2966' and 'Forrest' took up significantly more nitrate than the other cultivars ('Skiff', 'Franklin', 'Triumph', 'Stirling', 'Dampier', and 'Grimmett'). 'Stirlin' and 'Dampier' had the lowest total nitrate uptake (Table 4). The relationships between the increase in plant dry matter and uptake of nitrate over the 6 d for the 2 groups were not significant (Fig. 1a). There were significant linear relationships between the total nitrate uptake of the plants and the total dry weight at H2 (Fig. 1b), but comparison of the regressions showed that they are not significantly different from one another. Therefore, the two groups of cultivars showed statistically similar relationships between dry matter production and nitrate uptake. There were no significant differences in two indices of N use efficiency (TDM/ nitrate uptake, ΔDM/Δ nitrate) between cultivars (Table 4).

Experiment 2

There were significant differences between the nine barley cultivars in root, shoot and total plant dry weights at both harvests (Table 5). At the first harvest, 'Shannon'and 'Galleon' had significantly higher root dry weights than the other cultivars. The remaining cultivars did not differ significantly. At harvest 2, root dry weights of 'Prior A', 'Clipper', 'Chebec', 'Franklin', 'Schooner', 'Triumph' and 'Skiff' were not significantly different but those of 'Galleon' and 'Shannon' were again greater. Shoot dry weight was higher in 'Galleon', 'Shannon', 'Skiff' and 'Franklin' than in the others at first harvest. It was higher in 'Galleon' and 'Shannon' and the lowest in 'Chebec', 'Schooner' and 'Prior A' at the second harvest.

In Experiment 2, as in Experiment 1, the differences in growth were between cultivars rather than between the 2 groups. RGR was significantly different between cultivars and ranged from 14.1 d^{-1} in 'Schooner' to 9.7 d^{-1} in 'Shannon'. Within Group I cultivars, the RGR of 'Shannon' was significantly lower than 'Triumph' (Table 5). The high RGR for 'Schooner' is consistent with the results of the preliminary experiment. The growth rates of the semidwarf cultivars in Experiment 2 were similar to those in Experiment 1. The significant difference in growth rate is largely due to the value for 'Galleon'; there was no significant difference in the growth rates of the other cultivars.

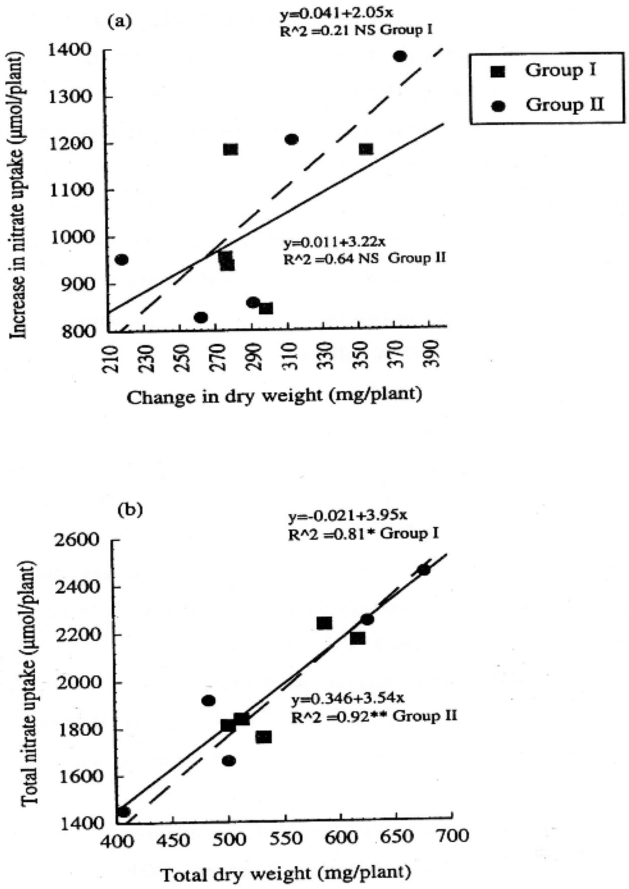

Fig. 1. Relationship between increase in dry weight and nitrate uptake over 6 d (a), and total dry weight and total nitrate uptake over 26 d for 10 barley cultivars (b) in Experiment 1.

Table 5. Effect of 1 mM nitrate supplied hydroponically on root, shoot and total dry matter production and growth rate of nine cultivars of barley in Experiment 2.

	Root DW ($mg\ plant^{-1}$)		Shoot DW ($mg\ plant^{-1}$)		Total DW ($mg\ plant^{-1}$)		RGR§ ($mg\ plant^{-1}$)	GR§ ($mg\ plant^{-1}$)
	H_1†	H_2	H_1	H_2	H_1	H_2		
Group I								
'Skiff'	87	167	191	395	279	562	11.79	47
'Franklin'	86	139	189	383	275	522	10.71	41
'Triumph'	69	151	169	386	239	537	13.61	50
'Shannon'	129	197	241	467	371	663	9.75	49
Group II								
'Schooner'	71	147	147	351	218	497	14.11	47
'Galleon'	122	234	268	538	390	773	11.44	64
'Clipper'	78	127	157	318	235	445	10,88	35
'Prior A'	66	122	149	295	216	416	11.63	33
'Chebec'	65	130	146	337	210	475	13.64	44
LSD (5%)	29	50	53	91	79	130	2.73	13

† H_1=Harvest 1, H_2=Harvest 2, RGR=Relative growth rate, GR=Growth rate.
§ Based on total dry weight.

Total nitrate uptake per plant differed between cultivars but nitrate uptake per g root dry weight did not. 'Galleon' had a significantly higher nitrate uptake than the other cultivars, while 'Prior A'had the lowest uptake (Table 6). The nitrate uptake over 6 d was significantly related to the

Table 6. Total nitrate content, increase in nitrate uptake and nitrate uptake per root dry weight in experiment 1.

	Total NO3-uptake ($\mu mol\ plant^{-1}$) (0-26 d)	NO3-uptake† ($\mu mol\ plant^{-1}$) (20-26 d)	Nitrate uptake (μmol root $DW^{-1}\ d^{-1}$) (20-26 d)	$\Delta DM/\Delta NO_3^-$§ uptake (20-26 d)	Total NO_3-uptake (0-26 d)
GroupI					
'Skiff'	1993	1248	3271	0.228	0.283
'Franklin'	1871	1145	3372	0.218	0.289
'Triumph'	1771	1109	3360	0.269	0.303
'Shannon'	2282	1413	2920	0.208	0.291
Group III					
'Schooner'	1654	1047	3292	0.265	0.300
'Galleon'	2485	1487	2836	0.259	0.311
'Clipper'	1563	953	3108	0.225	0.289
'Prior A'	1511	869	3062	0.244	0.275
'Chebec'	1589	1031	3368	0.262	0.310
LSD (5%)	480	297	NS	NS	NS

† Increase in nitrate uptake.
§ Increase in dry matter over increase in nitrate uptake over 6 d.

growth of the plants in Group III but not in Group I (Fig. 2a). However, there were positive relationships between total nitrate content and total plant growth for cultivars in both groups (I and III) (Fig. 2b). 'Galleon' was different from the other Group III cultivars because of its high dry matter production and high nitrate uptake. However, comparisons of the regressions in Fig. 2b found that the slopes and intercepts were not statistically different. Therefore, the relationships between nitrate uptake and plant dry matter for Groups I and III are similar. There were no significant difference between cultivars for either (TDM/nitrate uptake) or (ΔDM/Δ nitrate) (Table 6).

Experiment 3

The 8 barley cultivars differed significantly in dry matter production at both harvests (Table 7). Root dry matter production was significantly higher than the other cultivars in 'Shannon' at the first harvest. 'Weeah', 'Lara', 'WI-2728' and 'Franklin' had the lowest root dry weight at the first harvest. At the second harvest, root dry weight was higher in 'Shannon','Parwan' and 'Skiff' and lower in 'Franklin', 'WI-2869'and 'Lara'. Shoot dry weight did not differ between 'Shannon', 'Skiff', 'Parwan'and 'Triumph' but was significantly higher for these than the others at the first harvest. There were also no differences between 'Shannon', 'Weeah', 'Parwan'and 'Skiff' in shoot growth at the second harvest, but shoot dry matter was low in 'Triumph', 'Lara', 'WI-2728' and 'Franklin' (Table 7). Total plant dry weight at H_1 was not different between 'Shannon', 'Skiff', 'Parwan' and 'Triumph' but it was lower in 'Lara', 'Weeah', 'WI-2728' and 'Franklin'. At the second harvest, plant dry weight did not differ between 'Shannon', 'Weeah', 'Skiff' and 'Parwan'but was lower in 'Lara', 'WI-2728', 'Triumph' and 'Franklin' (Table 7).

The period of Experiment 3 was shorter than the other two experiments and the semi-dwarf cultivars showed lower growth rates and nitrate uptake than in the other two experiments. 'Shannon' and 'Skiff' had higher nitrate uptake than 'Triumph' and 'Franklin' which is consistent with Experiments 1 and 2. RGR was significantly different between cultivars due to the high RGR of 'Weeah', there were few significant differences (Table 7). There were also significant differences between cultivars in growth rate. 'Weeah' had a much higher growth rate than other cultivars (Table 8).

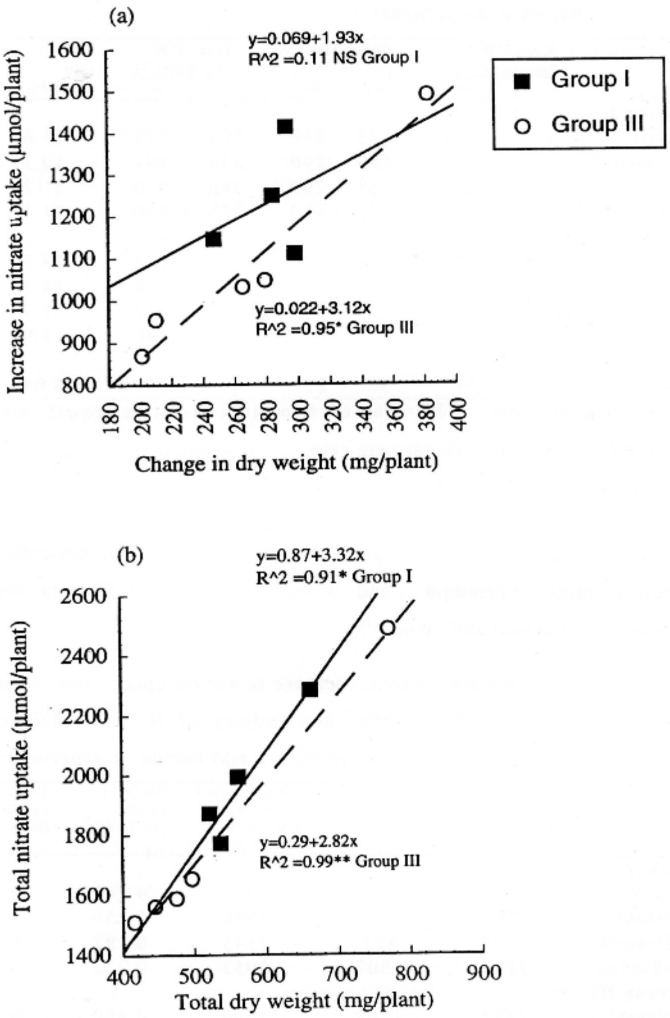

Fig. 2. Relationship between increase in dry weight and nitrate uptake over 6 d (a), and total dry weight and total nitrate uptake over 26 d for 9 barley cultivars (b) in Experiment 2.

Table 7. Effect of 1 mM nitrate supplied hydroponically on root, shoot and total dry matter production and growth rate of eight cultivars of barley in Experiment 3.

	Root DW (mg plant^{-1})		Shoot DW (mg plant^{-1})		Total DW (mg plant^{-1})		RGR§ (mg plant^{-1})	GR§ (mg plant^{-1})
	H_1†	H_2	H_1	H_2	H_1	H_2		
Group I								
'Skiff'	84	160	185	366	269	527	11.61	43
'Franklin'	62	105	153	290	216	394	10.31	30
'Triumph'	80	131	166	290	246	420	8.12	29
'Shannon'	110	172	192	410	303	590	11.37	48
Group IV								
'Weeah'	55	145	129	400	184	545	19.77	60
'Lara'	54	125	130	304	184	429	14.13	41
'WI-2728'	59	117	134	310	193	427	12.70	39
'Parwan'	83	172	174	368	257	540	11.97	47
LSD (5%)	23	24	30	82	43	91	6.08	16

† H_1 =Harvest one, H2=Harvest two, RGR=Relative growth rate, DW=Dry weight , GR=growth rate.

§ Based on total dry weight.

'Skiff', 'Lara', WI-2728, 'Franklin' and 'Triumph' did not differ in their growth rates. 'Triumph' and 'Franklin' were significantly lower than 'Shannon', 'Parwan' and 'Weeah'.

Table 8. Total nitrate content, increase in nitrate uptake and nitrate uptake per root dry weight, and indices of N use efficiency of 10 cultivars of barley grown with 1 mM nitrate in experiment 3.

	Total NO3-uptake (µmol plant^{-1}) (0-26 d)	NO3-uptake† (µmol plant^{-1}) (20-26 d)	Nitrate uptake (µmol root DW^{-1} d^{-1}) (20-26 d)	DM/NO3-§ uptake (20-26 d)	Total NO3-uptake (0-26 d)
GroupI					
'Skiff'	1806	1089	2991	0.240	0.297
'Franklin'	1286	757	2940	0.250	0.323
'Triumph'	1377	827	2545	0.192	0.303
'Shannon'	2142	1307	3053	0.222	0.277
Group III					
'Weeah'	1882	1008	3340	0.460	0.293
'Lara'	1439	863	3151	0.290	0.301
'WI-2737'	1242	638	2230	0.404	0.335
'Parwan'	1786	1047	2659	0.266	0.315
LSD (5%)	262	162	591	NS	NS

† Increase in nitrate uptake.

§ Increase in dry matter over increase in nitrate uptake over the 6 d.

There were a significant difference in the nitrate uptake per g root dry weight between cultivars (Table 8). 'WI-2728' had a significantly lower uptake than the other cultivars. There were no differences among 'Franklin', 'Skiff', 'Shannon', 'Lara' and 'Weeah' which were all high. Nitrate uptake per plant also differed between the barley cultivars. 'Shannon' had a significantly higher uptake than all the other cultivars except 'Weeah'. Uptake was low in 'Lara', 'Triumph', 'Franklin' and WI-2728. The linear correlation between the change in plant dry weight and uptake of nitrate over the 6 d was significant for the Group I but not for group IV (Fig. 3a). There were significant linear correlations between the total nitrate uptake and the total dry weight at H_2 (Fig. 3b). A comparison of the regression indicated the two Groups, I and IV, had the same slopes but different intercepts, i.e., the lines were parallel. Therefore, nitrate uptake by the cultivars in Group IV, was lower for the same amount of dry matter production, or conversely, dry matter production was higher when similar amounts of nitrate are taken up. This trend was seen in the indices of N use efficiency (ΔDM/Δ nitrate and TDM/nitrate), where the values for the Group IV cultivars tended to be higher than those of Group I, although the differences were not significant.

DISCUSSION

Overall, the present study found that in seedlings of barley cultivars, 1 mM nitrate nutrient solution promoted differences in dry weights of the root and shoot, nitrate uptake and nitrate assimilation. The major aim of these experiments was to examine whether there were any genetic differences in nitrate uptake in a range of barley cultivars. The result of the experiments suggested that at least two groups of cultivars could be identified as one group. The first group included 'Schooner' and 'Stirling' produced small seedlings and took up small amounts of nitrate. The second group was the semi-dwarf cultivars including 'Skiff' and 'Franklin', which took up greater amount of nitrate.

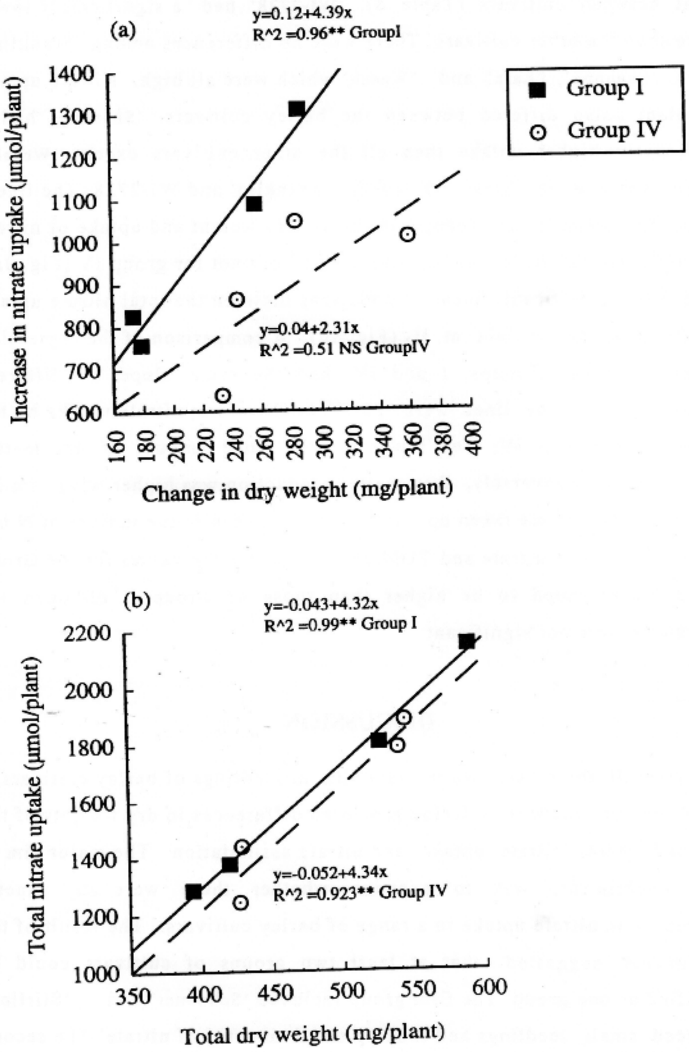

Fig. 3. Relationship between increase in dry weight and nitrate uptake over 6 d (a), and total dry weight and total nitrate uptake over 26 d for 8 barley cultivars (b) in Experiment 3.

The trend of increased nitrate uptake with greater plant dry weight over 6 d in Experiment 1 was not statistically different between the two groups (Fig. 1 a), which suggests that the differences between cultivars were related to the size of the plant. There were differences in dry matter production which were reflected in differences in nitrate uptake. In both the preliminary experiments and Experiment 1, there is a consistent result between cultivars, namely that 'Skiff' had high nitrate uptake and dry weight, but 'Stirling' had low nitrate uptake and dry weight (Tables 3 and 4).

The genetic differences in nitrate uptake appeared largely to be due to the differences in the size of the plants particularly roots, rather than differences in the ability of different cultivars to assimilate nitrate. There were few differences in the rate of nitrate uptake per g root, suggesting that differences in uptake were caused by the size of the root system. Perby and Jensen (12) also found that the differences in N uptake of barley cultivars were related to root size. In addition to root size, differences among cuitivar of barley in net ion uptake may also be due to different flux rates into and out of the roots (6, 7, 14).

In all experiments, cultivars which appeared to grow more vigorously, took up more nitrate. These results agree with those of Hackett (8) for barley and Reed and Hageman (13) for corn who found that high nitrate uptake was associated with a more extensive root system. Results from field experiments (4) show that at Northfield in 1991 dry matter production at 10 wk for 'Weeah' and 'Skiff' was higher than that of 'Stirling' and 'Schooner' Northfield 1991 was the most N-responsive site and also the site where dry matter production was lowest and most affected yields. Therefore, there was a different response to N in early growth between cultivars. The responses in early growth in 'Skiff' and 'Weeah' in this field experiment are consistent with the responses observed in the hydroponic studies, however, only 'Skiff' showed a response in grain yield to N; 'Weeah' was not responsive. Therefore, different levels of nitrate uptake in early growth are not always beneficial to grain yield. The yield responsiveness of cultivars will also depend on the characteristics of their response to environmental conditions during latter stages of growth, particularly to water and temperature stress.

CONCLUSIONS

Results from the experiments in a hydroponic system showed genetic differences in nitrate uptake between barley cultivars. The differences can be explained mainly by differences in plant growth. The differences in growth and nitrate uptake characteristic could be related to the pedigree of these cultivars, mainly through the size of the seedling. However, Group IV cultivars do appear to have physiological differences from the other three Groups. There were some consistencies in the results from the hydroponic studies and measurements of early vegetative growth in a field experiment (4) although the differences in vegetative growth may not necessarily be linked to yield. 'Skiff', 'Weeah', 'Stirling' and 'Schooner' all had high growth rates and nitrate uptake, but in the field experiments (4) the grain yield of 'Skiff' and 'Stirling' were responsive to N in grain yield, whereas the grain yield of 'Weeah' and 'Schooner' showed little or no response to N. Therefore, high vegetative growth early in the growing season, although promoting uptake of nitrate from the soils, is not always related to the final grain yield response. However, it is possible to have a cultivar such as 'Skiff' that can take up nitrate efficiently and which may be more responsive to increased nitrate in the soil.

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