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Grain yield, carbon isotope discrimination and mineral content in mature kernels of barley under irrigated and rainfed conditions

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Summary – The relationship between yield, carbon isotope discrimination and ash content in mature kernels was examined for a set of 13 barley (*Hordeum vulgare*) cultivars. Plants were grown under rainfed and well-irrigated conditions in a Mediterranean area. Water deficit caused a decrease in both grain yield and carbon isotope discrimination (Δ). The yield was positively related to Δ and negatively related to ash content, across genotypes within each treatment. However, whereas the correlation between yield and Δ was higher for the set of genotypes under well-irrigated ($r=0.70$, $P<0.01$) than under rainfed ($r=0.42$) conditions, the opposite occurred when yield and ash content were related, i.e. $r=-0.38$ under well-irrigated and $r=-0.73$, ($P<0.01$) under rainfed conditions. Carbon isotope discrimination and ash content together account for almost 60% of the variation in yield, in both conditions. There was no significant relationship ($r=-0.15$) between carbon isotope discrimination and ash content in well-irrigated plants, whereas in rainfed plants, this relationship, although significant ($r=-0.54$, $P<0.05$), was weakly negative. The concentration of several mineral elements was measured in the same kernels. The mineral that correlated best with ash content, yield and Δ , was K. For yield and Δ , although the relationship with K followed the same pattern as the relationship with ash content, the correlation coefficients were lower. Thus, mineral accumulation in mature kernels seems to be independent of transpiration efficiency. In fact, filling of grains takes place through the phloem pathway. The ash content in kernels is proposed as a complementary criterion, in addition to kernel Δ , to assess genotype differences in barley grain yield under rainfed conditions.

yield/barley/kernel/mineral content/carbon isotope discrimination

Résumé – Rendement en grain, discrimination isotopique du carbone et teneur en minéraux dans les grains mûrs d'orge en conditions irriguée et non irriguée. La relation entre la production, la discrimination isotopique et le contenu en cendres dans les grains mûrs a été examinée dans 13 cultivars d'orge (*Hordeum vulgare* L.). Les plantes ont été cultivées dans 2 conditions : l'une en déficit hydrique et l'autre en régime d'irrigation, en zone méditerranéenne. Le déficit hydrique a causé une diminution de la production et de la discrimination isotopique du carbone (Δ). La production a été positivement corrélée avec Δ et négativement avec le contenu en cendres, entre les génotypes de chaque traitement. Cependant, tandis que la corrélation entre la production et Δ a été plus haute dans l'ensemble des génotypes sous conditions d'irrigation ($r=0,70$; $P<0,01$) que chez les non irrigués ($r=0,42$), le contraire se produit quand la production et le contenu en cendres sont mis en rapport ($r=-0,38$ sous conditions d'irrigation et $r=-0,73$, ($P<0,01$) sous conditions de sécheresse). La discrimination isotopique du carbone et le contenu en cendres expliquent ensemble environ 60% de la variation dans la production dans les 2 conditions. Il n'y a pas eu de relation significative ($r=-0,15$) entre la discrimination isotopique du carbone et le contenu en cendres

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dans les plantes irriguées, tandis que dans les non irriguées, cette relation, bien qu'elle ait été significative ($r = -0,54$; $P < 0,05$), a été faiblement négative. La concentration de quelques éléments minéraux a été mesurée dans les mêmes grains. Le minéral le mieux corrélé au contenu en cendres, à la production et à Δ , a été le K. Pour la production et Δ , bien que la relation en K ait suivi le même schéma que la relation en contenu en cendres, les coefficients de corrélation sont plus bas. De cette façon, l'accumulation minérale dans les grains mûrs semble être indépendante de l'efficacité transpiratoire; en fait, le remplissage des grains a lieu à travers la voie du phloème. Le contenu en cendres des grains est proposé comme un critérium complémentaire, en plus du Δ des grains, pour fixer des différences génotypiques dans la production de grains d'orge en situation de déficit hydrique.

production/orge/grains/contenu en minéraux/discrimination isotopique du carbone

INTRODUCTION

Water-use efficiency (WUE), the ratio of CO₂ fixed to H₂O transpired, is an important plant attribute for growth in dry areas. Carbon isotope discrimination (Δ) is negatively correlated with WUE, and has thus been proposed as an integrated criterion for WUE selection in breeding programs for crop plants, since there is significant genetic variation in WUE within and between species (Farquhar and Richards, 1984; Farquhar *et al*, 1989).

Carbon isotope discrimination is positively correlated with intercellular CO₂ concentration (Farquhar *et al*, 1989). At first, low Δ appears to be an advantageous trait, especially in water-stressed environments, as it indicates a high WUE. However, low Δ has been associated with low yield and water-stress susceptibility in wheat (Morgan *et al*, 1993) and barley (Romagosa and Araus, 1991). In fact, higher stomatal conductance appears to allow higher photosynthetic rates, even when WUE decreases (Austin, 1987) and thus improves yield. Moderate positive correlations between mean grain yield and mature grain Δ have been reported in the same genotypes (Romagosa and Araus, 1991; Araus *et al*, 1993) for a set of environments of differing water deficits, even in the most severe. The isotope composition of the kernel at maturity integrates the C from photosynthesis during grain filling with that stored before anthesis.

Alternatively, plant mineral content may be a useful (*ie* cheaper and easier to develop) criterion in selection programs to improve transpiration efficiency since its correlation with WUE has been reported to be not much lower than that of Δ (Masle *et al*, 1992). Thus, Masle *et al* (1992) found a negative relationship between WUE and ash content (m_a) and a positive correlation between Δ and m_a , with-

in leaf blades of species with C₃ and C₄ pathways of photosynthesis. However, no study has been reported with m_a of kernels, even though they are currently used more than leaves for studies relating Δ and yield in cereals.

Here we describe the relationship between total ash content or the content of different minerals in kernels and Δ of the same kernels or grain yield for a set of barley cultivars grown under Mediterranean conditions, with varying water regimes.

MATERIALS AND METHODS

Thirteen cultivars of barley (*Hordeum vulgare* L) were grown during the spring of 1990 in the experimental fields of the Faculty of Biology, University of Barcelona, Spain. The soil was a mollic xerofluent with a sandy loam texture. The prevailing climate was Mediterranean. Plants were sown on January 24 at a seeding density of 250 seeds m⁻². The experimental design consisted of a randomized block with 4 replicates per cultivar and water regime divided into 20 plots (4.8 × 2 m), 4 genotypes per plot and 6 rows (20 cm apart) per genotype. At planting plots received 8 kg N ha⁻¹ as granular NH₄NO₃ (33.5% N) fertilizer, and 12 kg N ha⁻¹, 5.2 kg P ha⁻¹ and 10 kg K ha⁻¹ in the form of a compound granular commercial fertilizer. Granular NH₄NO₃ (33.5% N) fertilizer was additionally applied on March 2 and March 22, at the rate of 20 kg N ha⁻¹ each, resulting in a total of 60 kg N ha⁻¹.

All genotypes were grown under 2 water conditions: (i) rainfed with limited irrigation at sowing time and in mid-February, following the first fertilization and thereafter only water from rainfall; and ii) regularly watered, to attain normal growth and development. Anthesis took place between mid-April and the first week of May. The grain yield at maturity was recorded.

Kernels used for stable ¹³C isotope analysis were oven-dried and ground to a fine powder. The carbon isotope ratios (¹³C/¹²C) were determined by mass spectrometry by Isotope Services Inc,

Los Alamos, NM, USA. Values were expressed as $\delta^{13}\text{C}$ values, where:

$$\delta^{13}\text{C} (\text{‰}) = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000 \quad [1]$$

where R is the $^{13}\text{C}/^{12}\text{C}$ ratio. The standard for comparison was a secondary standard calibrated against Pee Dee belemnite (PDB) carbonate. Replicate samples differed by less than 0.10‰.

The value of the discrimination (Δ) against ^{13}C was obtained from the isotope ratio, δ_p , and δ_a (the carbon isotope composition of air, -7.85‰):

$$\Delta = \frac{\delta_a - \delta_p}{1 + \delta_p}$$

The ash content (m_a) in the powder was determined by burning it in a compact metallic block for digestion (RAIPA, SL, Spain, model MB-20) at 450°C for 8 h and weighing the residue. There were at least 3 replicates per cultivar sample, and approximately 3 g dry material was used per replicate. The ash content was expressed as a percentage of kernel dry weight. Nitric-perchloric (2:1) wet digestions were carried out on grain ash (3 ml acid: ~ 0.1 g ash) in an adapted microwave oven for 20 min at the highest power level (1200 W) to eliminate traces of organic matter. The ash was then dissolved in 25 ml nitric acid (5% volume). Contents of K, Na, Mn, Mg, Fe, Ca and Zn were later analyzed using inductively coupled plasma atomic emission spectroscopy (Polyscan 61E, Thermo Jarell Ash). Analyses were performed in the Servei d'Espectroscopia at the University of Barcelona. The values are means of 3 replicates per sample. Ion contents were expressed alternatively as ppm of dry weight (table I) or total content per kernel.

RESULTS AND DISCUSSION

A weak ($p < 0.1$) negative correlation was found between Δ and m_a in mature kernels for the rainfed treatment. No relationship was observed between the 2 parameters for the irrigated treatment (fig 1). Previous studies (Masle *et al*, 1992) reported a positive correlation between m_a and Δ in leaf dry matter. These different results suggest that mineral accumulation in the kernels is primarily regulated by a process other than transpiration and efficiency in the use of water.

The lack of a relationship between Δ and m_a under well-irrigated and rainfed conditions strongly suggests that mineral accumulation in mature kernels is insensitive to environmental changes that affect the transpirational stream, and thus the passive accumulation of mineral elements or WUE. Present results suggest that, in contrast to that reported for Δ of kernels (Condon *et al*, 1900; Morgan *et*

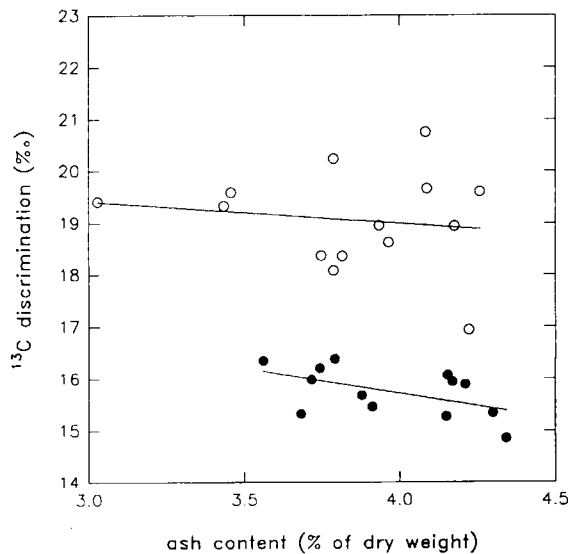


Fig 1. Relationship between ash content, per unit dry matter, and carbon isotope discrimination in mature kernels for a set of 13 barley genotypes grown under irrigated (\circ , $r^2 = 0.0221$) and rainfed (\bullet , $r^2 = 0.2922$) Mediterranean conditions.

al, 1993), mineral accumulation in the kernel is not related to the integrated WUE of the plant during the grain-filling period. In fact, minerals accumulate in kernels by phloem transport rather than passively from the transpiration stream. Walker and Lance (1991) reported that silicon concentration in plant (not kernel) samples of a set of barley cultivars correlated with Δ positively and more strongly in the field than in the glasshouse experiments, in which a weak negative correlation between parameters was observed. These authors suggested that, under mild glasshouse conditions, plants actively accumulate Si whereas, under higher evaporative demand in the field, Si accumulates passively by the transpirational stream.

Yield was negatively ($p < 0.05$) related to m_a in the rainfed treatment (fig 2). The negative relationship was not significant in the irrigated treatment. Of the mineral elements assayed (table I), the concentration of K per kernel dry matter best correlated with total kernel ash content, yield and Δ (table II). However, for yield and Δ , the relationship with K followed the same pattern as the relationship with ash content, but the correlation coefficients were lower.

The accumulation of carbohydrates in the grain depends on the photosynthetic rates during grain filling and on pre-anthesis storage, mainly in the internodes. On the other hand, mineral accumulation in the kernel de-

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Table 1. Kernel dry weight, ash content (% dry weight) and ion content in kernel (ppm of dry weight) measured in mature kernels. Values are means of at least 3 replicates (SE, below mean value) measured on 14 genotypes grown under irrigated (IR) conditions and on 13 of these genotypes grown under rainfed (R) conditions.

Cultivar	Kernel dry weight		Ash content (% DW)		Ion content (ppm of dry weight)													
	IR	R	IR	R	Mn IR	Mn R	Ca IR	Ca R	Na IR	Na R	Mg IR	Mg R	Zn IR	Zn R	Fe IR	Fe R	K IR	K R
Alexis	37.93	33.59	3.03	3.79	13.89	13.30	363.94	354.54	210.27	185.30	1075.35	943.60	36.17	48.69	45.90	41.90	5907.01	4584.40
Beka	40.53	32.87	0.07	0.17	0.34	2.25	7.06	37.86	4.25	43.78	20.09	166.44	0.62	11.12	0.99	5.35	110.45	775.50
EVI213	36.50	28.15	0.08	0.09	0.19	0.92	3.66	71.01	1.40	11.43	38.60	18.20	0.56	2.68	0.44	1.99	68.16	367.02
EVI215	34.27	34.95	0.03	0.15	2.50	1.77	33.72	25.64	19.79	10.89	176.87	36.63	8.49	1.16	5.18	1.35	1034.24	110.28
Zaida	46.42	31.82	0.21	0.03	0.17	0.60	9.65	9.60	1.39	1.06	21.96	36.62	1.10	0.98	0.47	0.73	288.29	33.73
Kym	36.17	32.15	0.08	0.08	0.41	0.89	26.84	9.82	8.57	4.67	67.73	23.34	2.78	1.84	2.05	1.21	342.51	156.97
Cameo	36.54	35.23	0.06	0.14	0.13	0.59	4.52	20.32	2.93	6.01	13.99	54.83	0.26	2.68	0.34	2.01	81.66	309.05
Dobla	37.07	34.30	0.11	—	0.65	—	22.30	—	4.25	—	67.10	—	1.59	—	2.45	—	263.10	—
ID 4016	41.29	28.75	0.14	0.13	0.34	0.43	8.64	25.96	3.31	3.07	17.44	39.07	0.83	2.36	0.80	1.23	117.96	209.83
Hatifi	46.23	38.35	0.14	0.05	1.24	1.63	37.72	164.44	9.89	12.68	94.42	103.30	3.35	3.53	2.59	14.87	207.17	137.67
Albacete	32.72	24.06	0.10	0.08	0.21	2.71	8.26	110.60	3.31	14.98	16.38	218.14	0.86	12.84	0.80	8.83	62.09	1056.44
Pane	61.90	39.95	0.08	0.19	0.42	0.44	19.43	23.79	2.94	6.47	43.79	33.33	2.34	1.61	1.66	3.62	197.74	253.97
Roxana	50.81	40.59	0.09	—	0.46	0.75	575.88	506.71	65.93	198.93	1264.43	1211.88	33.67	57.00	42.48	57.69	5120.49	5892.69
AD8	49.42	41.17	0.14	0.06	0.37	0.48	15.24	20.37	2.51	3.29	42.58	30.56	0.86	1.60	1.94	55.95	4898.94	5425.01
			4.18	3.68	13.10	16.64	454.04	440.74	53.12	73.97	1150.03	1198.13	34.23	47.62	36.04	62.91	4587.15	4721.86
			0.21	0.12	0.29	1.20	6.99	37.21	2.24	5.45	17.70	80.39	0.52	3.26	1.06	5.11	52.25	286.30

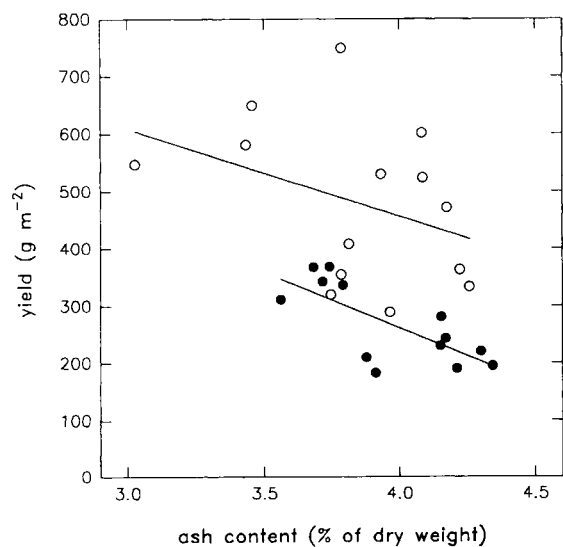


Fig 2. Relationship between ash content in mature kernels and grain yield for the set of genotypes and growth conditions shown in figure 1 (irrigated \circ , $r^2 = 0.1448$; rainfed \bullet , $r^2 = 0.5403$).

depends on current photosynthesis by the ear, translocation from the leaves, and also on minerals removed from the lower part of the plant after the onset of senescence (Wardlaw, 1990). Under rainfed conditions, photosynthesis is more restricted than translocation and the proportion of minerals to carbohydrates in kernels rises (see horizontal axis in figure 1) although the correlation with final kernel size may be lower. This is shown by the coefficient of determination of the relationship between the kernel dry weight and the absolute ash content per kernel, which was higher for the irrigated treatment ($r^2 = 0.87$; solid line in figure 3) than for the rainfed treatment ($r^2 = 0.57$; dotted line in figure 3). Similar differences between irrigated and rainfed conditions were found for the set of mineral elements studied (table III). In our study almost 60% of the variation in grain yield, in

Table II. Values of r^2 for correlations between K content per unit dry weight and total ash content, yield or carbon isotope discrimination (Δ).

	Total ash content DW^{-1}	Yield	Δ
K IR	0.021	0.001	0.009
K R	0.591	0.465	0.070

Correlations were performed using 13 genotypes, under either irrigated (IR) or rainfed (R) conditions. K, total mineral content and Δ were measured in mature kernels.

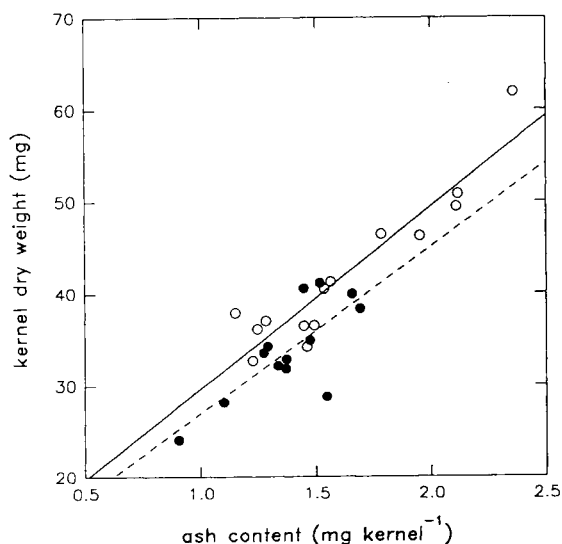


Fig 3. Relationship between ash content per kernel and kernel dry weight. The solid line corresponds to the linear regression fitted for irrigation treatment (\circ , $r^2 = 0.8712$) and the dotted line corresponds to the rainfed treatment (\bullet , $r^2 = 0.5736$).

both the irrigated and the rain-fed treatments, was explained by kernel Δ and m_a together (table IV). Taken together, these results suggest that the sources of dry matter for the kernel are differently affected by the water treatment. Under irrigation, the supply of carbohydrates to the kernel is enhanced by a longer grain-filling period, whereas under a shortage of water, the shorter photosynthetically active period brings about an increase in the mineral to carbohydrate ratio, as observed above.

Table III. Values of r^2 of the correlations between amount of mineral per kernel and total ash content per kernel.

Mineral	Total ash content	
	IR	R
Mg	0.773**	0.746**
Zn	0.468	0.331
Fe	0.555*	0.242
K	0.507	0.471
Mn	0.590*	0.550
Ca	0.666*	0.285
Na	0.020	0.037

Correlations were performed using 13 genotypes, under either irrigated (IR) or rainfed (R) conditions. Total ash content and total mineral content were measured in mature kernels. * $p < 0.05$; ** $p < 0.01$.

Table IV. Percentage of yield variation among genotypes explained by carbon isotope discrimination and ash content (% dry weight).

	<i>Irrigated</i>	<i>Rainfed</i>
Carbon isotope discrimination (%)	48.75	17.71
Carbon isotope discrimination + ash content (%)	56.57	56.68

Calculations were performed by fitting a multilinear regression model using PC-NCSS.

These results suggest that m_a from kernels may be considered as a complementary criterion to assess genotype differences in cereal grain yield, particularly under rainfed conditions.

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