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Genotype × Environment Interaction in the Andean Grain Crop Quinoa (*Chenopodium quinoa*) in Temperate Environments

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With 4 tables

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Abstract

Ten varieties of quinoa with origins ranging from latitude 39° S to 12° S and from sea level to an altitude of 3,800 m were grown on two soil types in two years in Cambridgeshire, England, in order to assess the extent and nature of genotype × environment (G × E) interactions and identify genotypes suited for cultivation at temperate latitudes. There was evidence that varieties differed in their susceptibility to waterlogging during germination. Plant height was strongly influenced by competition with weeds, and varieties differed in their susceptibility to this. The number of days to anthesis and to maturity were strongly dependent on the variety, but these periods were generally longer following an earlier sowing. The grain yield was also strongly dependent on the variety, but weed competition, a micronutrient deficiency and bird damage affected the varieties differently. Varieties originating at high latitudes gave the highest yields, about 5,000 kg/ha. Earliness and yield were strongly associated at the level of variety means, but the pattern of G × E interaction differed among the variables measured.

Key words: *Chenopodium quinoa* — novel crop — performance — genotype × environment interaction

In the evaluation of quinoa (*Chenopodium quinoa*) for use as a break crop between cereal crops in temperate agriculture, large effects of sowing date on yield were found in one variety, and there were variety × sowing date interaction effects on several other characteristics (Risi and Galwey 1991). There is evidence for the importance of environmental influences from other studies. In the Andes, where the crop originated, high altitude and low temperature were associated with a long growth period and high grain yield (Raez 1956, Montenegro 1976), and late sowing reduced growth period, plant height and yield (Flores 1977). Yield, plant height, growth period, seed size and saponin content all varied between accessions and locations in Colorado, USA (McCamant 1985). None of these investigations refers explicitly to genotype × environment (G × E) interaction, but when the main effects are so prominent it is unlikely that the interaction is absent.

The range of environments in which quinoa might be grown in Britain is narrower than in the studies cited above, but G × E effects are nevertheless likely to be important in the development of quinoa. In order to determine the pattern of such effects, a range of genotypes rather broader than would be considered for use in British agriculture was studied at two distinctive sites over two growing seasons.

Materials and Methods

Sites and weather: Trials were sown in the 1983 and 1984 growing seasons at the University Farm, Cambridge and at the Arthur Rickwood Experimental Husbandry Farm, Mepal, Cambridgeshire. Although these sites are only 20 miles apart, their soils are very different, that at Cambridge being a fine sandy loam whereas that at Mepal is an alkaline peat with high organic matter content and a large popula-

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Table 1. Characteristics of the quinoa varieties studied

Name	Ecotype[1]	Growth period (days)[2]	Seed colour	Seed saponin content
Chewecca	Altiplano	180	white	low
Linea de Alto	Probably Altiplano	—	white	high
Rendimento Puno 13 (LAR-13)				
Kanccolla	Altiplano	180	white	fairly low
Tahuaco 1	Probably Altiplano	—	white	high
Blanca de Julí	Altiplano	180	white	low
Sajama	Altiplano	154	white	almost none
UNC-20	Valley	—	white	high
Baer	Sea-level	109—129	yellow	high
Faro	Sea-level	119—140	yellow	high
Amarilla de Maranganí	Valley	200	yellow	high

[1] According to the classification of TAPIA, MUJICA and CANAHUA (1980).
[2] Determined in the variety's place of origin.

tion of weed seeds. In 1983 an exceptionally cold, wet spring was followed by a hot, dry summer, but in 1984 the weather was closer to the average.

Varieties and agronomic management: The varieties used are described in Table 1. Their origins range from latitude 39° S to 12° S and from sea level to an altitude of 3,800 m. The experimental plots were ploughed in the autumn and again in the spring, and were levelled and cultivated. Before the final cultivation, 375 kg/ha of 20 : 14 : 14 compound fertilizer was applied broadcast, corresponding to 75 kg/ha of N, 53.5 kg/ha of P_2O_5 and 53.5 kg/ha of K_2O. In 1983 the trial at Cambridge was sown on 12 April, that at Mepal on 27 April, and in 1984 the dates were 16 March and 23 April respectively. In each trial, each variety was sown in three replications in a randomized complete block design in plots consisting of four 3 m rows 0.4 m apart, so that the area of the plot was 3.2 m^2. The density of the seed within the row was 0.6 g/m, equivalent to a sowing density of 15 kg/ha. Seeds were hand sown and lightly covered. Seedlings were protected from bird attack using rotating bird scaring devices, compressed gas cannon and a humming line. The last was the most effective. Plots were hand weeded, and those showing symptoms of micronutrient deficiency were sprayed with a foliar feed. Plots in which the plants were still green by mid November were harvested then, and the plants were dried in a heated glasshouse before threshing. The following characteristics were determined in the two central rows of each plot: number of plants/m^2; plant height (m); days to anthesis (scored when 50 % of the plants had reached this stage); days to maturity (scored in the same way); seed yield (kg/ha).

Statistical methods: The trials were treated as having a split plot design, the blocks within each trial being the main plots. Year and location were the main plot factors and variety was the subplot factor. The components of variance due to variety, year, location and the interactions of these factors were calculated as described by COMSTOCK and MOLL (1963): however, with only four environments, it is necessary to interpret these components with caution. The stability variance (σ_i^2) — that is, the G × E variance associated with each variety (SHUKLA 1972) — was also calculated.

Results

Plant population is strongly dependent on the main effect of years and there is a large contribution from the variety × year component

Table 2. Variance components of variables recorded[1]

Variance component	No of plants/m²	Plant height (m)	Days to anthesis	Days to maturity	Grain yield (kg/ha)
Location (L)	1.427***	−0.02481	15.767	19.013	54744
Year (Y)	553.817***	−0.02402	−3.111	−7.423	−40366
L × Y	−2.483	0.05935***	8.921***	50.525***	102510***
Main plot error MS	74.480	0.00326	2.375	3.633	59073
Variety (V)	13.466	0.01032***	76.543***	531.768***	1839637***
V × L	14.490	−0.00367	−2.025	1.831	52809
V × Y	156.792***	−0.00124	−0.278	3.390	84258
V × Y × L	10.030	0.00932***	4.566***	18.351***	220571***
Sub-plot error MS	55.370	0.00465	2.375	6.170	28568

[1] Asterisks indicate the significance of the corresponding term in the analysis of variance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

(Table 2). The estimate of the location × year component is negative and its true value is therefore presumed to be zero. The mean values of the number of plants/m² show that the plant population was lower in 1983 than in 1984 (Table 3). This is because the seed used in 1983 came from different sources and had variable viability, whereas that used in 1984 was harvested at Cambridge in the previous year and its viability was high and uniform. There was no significant difference in plant population between the locations despite the fact that weed competition was more intense at Mepal than at Cambridge, especially in 1983. There was a highly significant variety × year interaction, due to the variable viability of the seed used in 1983.

Some of the possible causes of variation in plant population are of real interest, but the variation in initial seed viability is merely troublesome. The correlations between plant population and other characteristics are considered later: fortunately they are not strong at the G × E level.

The substantial location × year component of variance for plant height indicates that each environment needs to be considered independently. The variety × location × year component is of about the same size as the variety component, indicating that G × E interaction effects are about as large as the main effects of genotype. Plants were on average shorter in 1983 than in 1984, mainly due to the weather, which made weeding difficult at Mepal that year. In 1984, however, plants were shorter at Cambridge than at Mepal, probably due to a deficiency of magnesium or another micronutrient, which affected plants of 'Baer', 'Faro' and 'Amarilla de Maranganí'. Differences between varieties are mainly due to their ecotype, the valley varieties 'Amarilla de Maranganí' and 'UNC-20' being the tallest. The variety × location × year interaction is highly significant.

The number of days from sowing to anthesis depends mainly on the variety, though variety also interacts significantly with the environmental factors. The Sea-level varieties 'Baer' and 'Faro' flowered earliest, confirming that they are the best adapted to high latitudes (Risi and Galwey 1989). This was expected, since they originate at latitudes of 37—39° S in Chile (Etchevers and Avila 1981), and had already

Table 3. Mean values and stability variance (σ_i^2) of variables recorded

	No of plants/m^2		Plant height (m)		Days to anthesis		Days to maturity		Grain yield (kg/ha)	
	Mean	(σ_i^2)	Mean	(σ_i^2)	Mean	(σ_i^2)	Mean	(σ_i^2)	Mean	(σ_i^2)
Baer	211.83	49.18	1.493	0.00617	66.25	2.839	153.67	59.98	5142	315194
Faro	204.08	88.48	1.485	0.00204	73.67	2.408	164.42	7.97	4699	883758
Amarilla de Maranganí	230.58	64.96	1.612	0.00541	86.25	2.173	203.67	77.26	4309	75276
Chewecca	213.58	35.43	1.584	0.00498	85.08	1.921	199.42	38.48	3271	873975
LAR Puno 13	228.17	433.48	1.358	0.00334	87.00	0.400	212.08	3.33	3247	54108
Kanccolla	221.17	176.71	1.431	0.00849	85.00	5.778	207.00	6.75	2976	38001
Tahuaco 1	210.75	66.70	1.458	0.00637	88.58	3.417	218.00	1.87	2639	280262
Blanca de Julí	199.25	242.14	1.505	0.01260	87.33	0.045	213.08	2.87	1916	33024
Sajama	204.08	91.85	1.486	0.00014	85.17	3.230	208.08	11.17	1976	294506
UNC-20	213.58	35.14	1.724	0.01884	98.83	12.193	226.00	5.31	538	45140
SE_{Diff}	3.038		0.02785		0.629		1.014		69.0	
Chi square		9.11		12.52		16.99*		20.37*		18.10*
Cambridge	212.87		1.563		87.50		202.25		3303	
Mepal	214.55		1.464		81.83		195.83		2840	
1983	197.05		1.460		83.48		197.55		2994	
1984	230.37		1.567		85.15		203.53		3148	
SE_{Diff}	1.576		0.01042		0.281		0.348		44.4	

been selected for early maturity in Northern Europe (C. L. A. LEAKEY, pers. comm.). The period from sowing to anthesis was slightly shorter in 1983 than in 1984, and shorter at Mepal than at Cambridge, confirming that anthesis occurs more quickly following later sowings (RISI and GALWEY 1991).

The components of variance of the number of days to maturity follow a similar pattern to those of the number of days from sowing to anthesis. Again, the period was shortest in the Chilean varieties, and slightly shorter after later sowings. The Chilean varieties are better adapted to British environmental conditions, but are also earlier maturing than the others in their respective places of origin. All the varieties took longer from sowing to maturity in Britain than in their places of origin, with the exception of 'Amarilla de Maranganí'. This suggests that this variety is insensitive to long days — a characteristic much needed for adaptation of quinoa for cultivation in temperate latitudes.

Grain yield is strongly dependent on the variety, but also has fairly large variety × year × location and year × location components of variance. Competition with weeds at Mepal in 1983 lowered the yield in that trial, whereas the yield at Cambridge was lower in 1984, in spite of the earlier sowing date in that year, probably because of the micronutrient deficiency. Although there are interactions of varieties with environments, 'Baer' gave consistently high yields, averaging 5,142 kg/ha of seed, and the yields obtained from 'Faro' and 'Amarilla de Maranganí' were also high. The low yield obtained from 'UNC-20' probably reflects the poor adaptation of this variety to British environmental conditions and not its potential in the Andes. It is a highly branched variety with a relatively small terminal inflorescence, and at harvest only this had matured.

The chi-square statistics for BARTLETT's (1937) test of homogeneity of stability variances indicates that the varieties differ in their stability with regard to days to anthesis, days to maturity and grain yield, but not with regard to number of plants/m^2 and plant height (Table 3). This might suggest that as plant development proceeds, a characteristic pattern of interaction with environment starts to be expressed by each variety. However, the varieties with the greatest stability variances are not

Table 4. Correlations, in different strata of the analysis, between the variables recorded

		Number of plants/m^2	Plant height	Days to anthesis	Days to maturity
Plant height	Variety	−0.0405			
	Var. × Environm.	0.1262			
Days to anthesis	Variety	0.1804	0.3985		
	Var. × Environm.	0.2182	−0.2986		
Days to maturity	Variety	0.1832	0.1838	0.9614***	
	Var. × Environm.	−0.1394	0.1287	0.1006	
Yield	Variety	0.2461	−0.3403	−0.8579***	−0.8380***
	Var. × Environm.	−0.1148	0.0276	0.2542	0.1579

the same for each variable recorded: for days to anthesis, 'UNC-20' has the greatest variance, for days to maturity, 'Baer' and 'Amarilla de Maranganí', and for grain yield, 'Faro' and 'Chewecca'. These results also show that varieties of the same ecotype do not necessarily have the same pattern of interaction with environment.

The correlations presented in Table 4 confirm that there are no strong associations at the variety × environment level between the variables recorded. They do however confirm the existence of a strong association, in the main effect of variety, between early flowering, early maturity and high yield.

Discussion

Despite the strong correlations between the variety means for earliness and yield, the pattern of the G × E interaction differed considerably from one variable to another. The most straightforward pattern was that of the number of days from sowing to maturity, which was largely determined by the variety but generally greater in the earliest-sown trial, with some varieties showing this tendency more strongly than others. A similar pattern in the number of days to anthesis was complicated by the dependence of this variable on the precise timing of periods of sunshine. The pattern of G × E interaction was less easily interpreted in the case of yield, suggesting that several environmental variables had important effects. The main effect of varieties was also substantial. As expected, the Chilean varieties, pre-adapted to high latitudes, gave consistently high yields, but the high yield of the Valley variety 'Amarilla de Maranganí' was more surprising.

The environmental effect on plant height was more important, relative to the effect of variety, than in the case of the three variables discussed above. The plants were shorter in the trial in which competition with weeds was most intense, some varieties perhaps showing this tendency more strongly than others. Besides sowing date and weed competition, other environmental variables that appeared to affect the varieties differentially were waterlogging during germination, soil fertility, in particular a deficiency of an unidentified micronutrient, and damage by birds. The yields of the low-saponin varieties 'Chewecca' and 'Sajama' were sharply reduced by birds at Mepal in both years because these trials were not netted. No bird damage to the other varieties was observed at Mepal, confirming the efficacy of saponins in protecting the plants from attack. The trials at Cambridge had to be netted due to their proximity to urban areas, to avoid the severe damage that would otherwise have been caused by birds even to the high-saponin varieties.

Although further experiments would be needed to examine fully the effects of any one of these variables, the present investigation shows that even a limited range of environments can, if chosen with care, provide a good deal of insight into the factors which must be taken into account when adapting a crop to a new region and agricultural system.

Zusammenfassung

Genotyp × Umwelt-Interaktion andiner Reismelde (*Chenopodium quinoa*) in gemäßigten Zonen

Zehn Sorten der Reismelde wurden auf zwei verschiedenen Böden 2 Jahre lang in Cambridgeshire, England, angebaut, um Art und Ausmaß der Genotyp × Umwelt-Wechselbeziehung (G × E) zu bestimmen. Ferner sollten die Genotypen ermittelt werden, die sich für einen Anbau in gemäßigten Zonen eignen. Die Sorten stammten aus Höhenlagen zwischen 0 und 3800 m. Gebieten zwischen den Breitengraden 39° S und 12° S. Es gab deutliche Hinweise dafür, daß zwischen den Sorten bei der Samenquellung während des Keimungsprozesses Unterschiede vorhanden waren. Die Höhe der Pflanzen hing stark vom konkurrierenden Unkraut ab, das die Sorten in unterschiedlichem Maße beeinflußte. Ebenso war die Zahl der Tage bis zur Blüte und bis zur Erntereife stark sortenabhängig; in der Regel verlängerte sich dieser Zeitraum nach früher Aussaat. Auch der Kornertrag war stark sortenbedingt; allerdings wurden die Unterschiede hier durch den konkurrierenden Einfluß des Unkrauts, durch einen Mangel an Mikronährstoffen und durch Vogelfraß verursacht. Die Sorten, die aus Gegenden hoher Breitengrade stammten, wiesen mit etwa 5000 kg/ha die höchsten Erträge auf. Die Mittelwerte der Sorten für Frühzeitigkeit und Ertrag waren eng miteinander korreliert. Die Unterschiede zwischen den G × E-Wechselwirkungen der gemessenen Merkmale waren jedoch beachtlich groß.

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