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## Stability of quantitative traits in quinoa (*Chenopodium quinoa*)

Received: 10 October 1995 / Accepted: 3 November 1995

**Abstract** The stability of various descriptive characters was studied over a 5-year period in 14 lines of quinoa (*Chenopodium quinoa* Willd.) to determine the most appropriate time in a breeding programme when selection for these characters could be performed, and which lines could serve as potential parents. Various measures of stability were employed to analyse these data, including those proposed by Francis and Kannenberg (1978) and Lin and Binns (1988), appropriately modified for the purpose of this investigation. From these results it was concluded that selection for height, inflorescence size and developmental stage could be satisfactorily performed at an early stage of the breeding programme. For saponin content, however, the measuring techniques available were too insensitive to enable a recommendation to be made. Potential parents were identified in this material for use in the development of varieties suitable for North European conditions.

**Key words** *Chenopodium quinoa* · Genotype-environment interaction · Quinoa · Stability · Superiority

### Introduction

Genotype × environment (GE) interactions, which occur whenever the phenotypic response to environmental change differs among genotypes, complicate the selection process among genotypes evaluated in different environments. The presence of GE interaction automatically implies that the behaviour of genotypes in a trial depends upon the particular environment in which they are grown (Hill 1975). Consequently, relative rankings may differ, or absolute differences may change

between environments. In recent years, several methods have been proposed for the identification of superior genotypes, even in the presence of GE interaction.

A measure of general cultivar superiority for cultivar × location data was defined by Lin and Binns (1988) in terms of the distance mean square between the cultivar's response and the maximum response averaged over all locations. Since the maximum response is the upper boundary in each location, a low mean square indicates high relative stability, and thus general superiority of the test cultivar. This approach was used by Lin and Binns to identify generally and specifically adapted types among a set of barley cultivars, whilst Helgadóttir and Kristjansdóttir (1991) employed the method for a similar purpose in timothy (*Phleum pratense*).

Another approach often employed is to select phenotypically stable genotypes whose performance over environments is relatively constant. Such genotypes, described by Becker and Léon (1988) as static, may often be low yielding, however, because they are unable to exploit high-yielding environments (Finlay and Wilkinson 1963). The stability of this type, measured as the environmental variance, depends on the environments but not on the other genotypes included in the trial. It provides no information, however, on the response pattern of genotypes over the test environments. Coefficients of variation (CV) may also be used, although it could be argued that a low CV can be obtained either from a low variance or a high mean yield. Therefore, Francis and Kannenberg (1978) suggested that the combined use of CV and yield could be more informative.

In contrast to the static concept outlined above, the dynamic concept of stability is based on a predictable response to environments. The most widely used technique here is the linear regression over environments first introduced by Yates and Cochran (1938) and independently rediscovered by Finlay and Wilkinson (1963), Eberhart and Russell (1966) and Bucio Alanis (1966). In this concept a stable genotype has low residual devi-

Communicated by P. M. A. Tigerstedt

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ations from its linear response or sensitivity to environments (Breese 1969; Becker and Léon 1988). The linear regression approach is useful for comparing a specific set of genotypes, but because the mean of all genotypes is widely used as the standard response in each environment, inferences from this type of stability require caution unless the genotypes are a representative sample of those grown in the area in question (Lin et al. 1986).

Quinoa (*Chenopodium quinoa* Willd), a predominant inbreeding species native to the Andean region of South America, is currently being investigated for its suitability as a commercial crop in Europe, particularly for set-aside and marginal areas. This paper presents the results of an investigation into the stability of some important developmental and quality characters in this species that was conducted in order to identify material which could serve as potential parents in future breeding programmes.

## Materials and methods

### Experimental

The material used in these experiments consists of 14 lines of quinoa that have been selected for agronomic performance and uniformity under Danish conditions. A summary of the origin and morphology of these lines is presented in Table 1 (see Risi and Galwey 1989; Jacobsen and Stølen 1993, for further details).

Experiments were conducted on a sandy loam soil at the research station of the Royal Veterinary and Agricultural University, located close to Copenhagen, Denmark. Sowing took place in late April each year, when the soil temperature was about 8°C. Nitrogen was supplied as a top-dressing approximately 2 weeks after emergence at a rate of 120 kg/ha. In 1988 and 1989, the experiments were performed in progeny rows of lengths 2 and 3 m, respectively, spaced 50 cm apart. From 1990 onwards, sufficient seed was available to sow replicate plots of 15 m<sup>2</sup> for each line. In 1990 and 1991, row spacing was 50 cm, while in 1992 rows were spaced 25 cm apart. Weeds were controlled mechanically. All experiments were laid out as randomized complete blocks with three replicates.

The characters recorded were height, inflorescence size, developmental stage and saponin content. Height and inflorescence size were measured after growth had ceased at the beginning of August. Developmental stage, i.e. earliness, was determined by scoring at week 32. Saponin content was assessed either by bitterness in a taste test of mature seeds, on a scale from 0–10, or, as in 1992, by an afrosimetric method that entailed the estimation of foam development (Kozio

1990). The taste test was originally chosen because for human consumption bitter taste is a negative characteristic (see discussion in Price et al. 1987; Jacobsen 1992).

The environmental spectrum covered by this investigation was very wide, due to marked climate differences between the seasons. Thus, in 1988 total rainfall in the growing season was above normal, although June and August were relatively dry. 1989 was dry from May to September, with the exception of the second half of August. In 1990 precipitation in May, June and July was below, above and below normal, respectively. In 1991 the spring was wet and cold, especially April and June, while the rest of the growing season was normal. 1992 was a year of severe drought, especially in May and June, though April was cold and wet.

### Statistical

For the analyses of variance the model used was

$$Y_{ijk} = \mu + \alpha_i + (\epsilon_j + \tau_{jk}) + (\alpha\epsilon)_{ij} + \epsilon_{ijk} \quad (1)$$

where  $Y_{ijk}$  is the observed value of the character for the  $i$ th line in the  $j$ th environment and the  $k$ th replicate within that environment;  $\mu$  is the overall mean;  $\alpha_i$  is the effect of the  $i$ th line,  $\epsilon_j$  the effect of the  $j$ th environment;  $(\alpha\epsilon)_{ij}$  is the interaction of the  $i$ th line in the  $j$ th environment;  $\tau_{jk}$  is the replicate effect; and  $\epsilon_{ijk}$  is the error term. The factors were analysed independently from each other by either a partial or a successive test. In the former, the sum of squares (SS) for a variable is the reduction in error SS due to adding that variable to the model that already contains all the other variables in the model list. When a successive test is used, the SS in the reduction in error SS due to adding a certain variable to a model that contains all the variables preceding the one of interest in the model statement. For regression analyses a successive test provides the most useful information (Littell et al. 1991), while a partial test is used for the analyses of variance.

The original superiority measure  $P_i$  of the  $i$ th line, as suggested by Lin and Binns (1988), was calculated from the formula

$$P_i = \sum_{j=1}^n (X_{ij} - M_j)^2 / (2nr)$$

where  $X_{ij}$  is the attribute value of the genotype in the  $j$ th environment,  $M_j$  is the maximum value in the  $j$ th environment,  $n$  is the number of environments and  $r$  is the number of replicates per environment.

For several of the characters recorded in our experiment, however, a low expression is required. Consequently,  $M_j$  has been replaced by  $O_j$ , the optimum value in the  $j$ th environment, which will be the genotype with the highest or lowest expression, depending upon the character. Since  $P_i$  is the distance mean square from  $M$  or  $O$ , the smaller this value the greater is the coincidence between the optimum and test genotype response. It can be regarded as a measure of superiority in the sense of general adaptation (Lin and Binns 1988).

**Table 1** Origin and morphology of quinoa lines used in this investigation (Jacobsen and Stølen 1993)

Line <sup>a</sup>	Origin	Colour of inflorescence	Developmental stage for inflorescence colour expression	Leaf size
1	205 Baer × Faro (Chilean cultivars)	Red	16–17 (67–100% seed set)	Large
2	210 Kcancolla × Amarilla de Marangani (Peruvian cultivars)	Light red	15 (50% seed set)	Large
3	224 Germplasm collection	White	11 (onset of floral dehiscence)	Small
4–13	227 Field selection from Chilean material 230–231 233–234 238–240 244–245	Orange → red	14–15 → 16–17 (33–50% seed set → 67–100% seed set)	Medium
14	Olav Standard variety	Yellow	15 (50% seed set)	Large

<sup>a</sup> First column (numbers 1–14): serial numbers for the lines used in this experiment. Second column: breeder's codes

An alternative measure of overall superiority, here designated  $P(o)_i$ , may be computed from

$$P(o)_i = \left[ \sum_{j=1}^n (X_{ij} - O_j)^2 \right] / (2nr)$$

were deviations between  $X_{ij}$  and  $O_j$  are summed over environments before squaring.

If selection is based on  $P_i$ , however, a genotype specifically adapted to certain environments may be discarded. Therefore, Lin and Binns advocate the calculation of a pairwise GE interaction MS between the maximum and each genotype. If this MS is not significantly larger than the error, differences from the optimum are comparable for all environments, and the  $P_i$  value is an appropriate indicator of superiority. A significant GE interaction, on the other hand, implies differences in the response pattern, which would then require a more detailed investigation. Thus, a distance mean square is calculated for the  $i$ th genotype in each environment. After summation over environments the  $P(o)_i$  value is subtracted to give a heterogeneity value,  $P(het)_i$ , where

$$P(het)_i = \sum_{j=1}^n (X_{ij} - O_j)^2 / (2r) - \left[ \sum_{j=1}^n (X_{ij} - O_j)^2 \right] / (2nr).$$

If the individual deviations from the  $O_j$  value are the same in each environment,  $P(het)_i$ , which is equivalent to Lin and Binns' pairwise GE interaction mean square, will equal zero. Lin and Binns' original superiority index and the alternative suggested here will give similar rankings of the genotypes. The revised index is expected to identify fewer superior genotypes, however, because it squares the sum of the deviations over environments between the candidate and optimum genotype, whereas Lin and Binns' measure sums the squares of the deviations in each environment. Furthermore, Lin and Binns' measure is based on  $n$  *df*, while the modified version has only a single *df*. The modified index will therefore yield a more conservative test for superiority.

Like Lin and Binns' original measures, a low  $P(o)_i$  value and a non-significant  $P(het)_i$  suggest general adaptation. The significance of the modified distance mean squares is assessed against the experimental error, which is used merely as a cut-off point, because their distributions are unknown.

The model used for the linear regression was

$$Y_{ij} = \mu_i + (1 + \beta_i)e_j + \delta_{ij} \tag{2}$$

where  $Y_{ij}$  is the observed variable of the  $i$ th line in the  $j$ th environment,  $\mu_i$  is the mean of the  $i$ th line over all environments,  $\beta_i$  is the linear regression coefficient that measures the response or sensitivity of the  $i$ th line to environmental change,  $e_j$  is the environmental index obtained as the mean of all lines in the  $j$ th environment, and  $\delta_{ij}$  is the deviation from the fitted regression of the  $i$ th line in the  $j$ th environ-

ment. Regressions may differ in level (mean over environments), slope (regression coefficient) and deviation from regression.

A  $t$ -test was used to determine whether the regression coefficient for the  $i$ th line differed significantly from either 0 or unity. The deviation for the  $i$ th line ( $s_{ei}^2$ ) was calculated as

$$s_{ei}^2 = [\text{residualSS}_i / (n - 2)] - s_e^2 / r$$

where  $s_e^2$  is the experimental error and  $r$  is the number of replicates. To test whether the residual deviations for the  $i$ th genotype about its fitted regression line were significant, we used an approximate  $F$ -test (Eberhart and Russell 1966), where

$$F = \frac{(\text{residualSS}_i / n - 2)}{s_e^2 / r}$$

Although only limited use of the linear regression analysis has been made here, it has nevertheless been used in conjunction with a modified version of the Francis and Kannenberg approach, for which the environmental variance ( $s_x^2$ ), standard deviation ( $s_x$ ) and coefficient of variation ( $CV = s_{x(x)}$ ) were also used as measures of stability. Estimation of variance components was performed by the restricted maximum likelihood procedure (SAS/STAT 1988). Total variation was the sum of variance components for lines, environments, replicates within environments, like x environment and error:

$$\sigma_{\text{total}}^2 = \sigma_L^2 + \sigma_Y^2 + \sigma_R^2 + \sigma_{LY}^2 + \sigma_e^2 \tag{3}$$

## Results

Table 2 presents the line means and standard deviations over years of the recorded characters. From the corresponding analyses of variance, differences between lines and years (environments) were significant for all recorded characters (Table 3). Genotype-environment interactions were likewise significant for all characters, with variance components accounting for between 1% (height) and 16% (saponin content) of the total variation.

Table 4 shows  $P(o)_i$  and  $P(het)_i$  for all lines, with the optimum value at the top, followed by lines ranked by increasing distance from the optimum. For developmental stage and inflorescence size the optimum value is the maximum, while for height and saponin content it is the minimum, calculated as the average over years of those

**Table 2** Means ( $\bar{x}$ ) and standard deviations over years ( $s$ ) for the 14 lines

Line	Height (cm)		Inflorescence size (cm)		Developmental stage		Saponin	
	$\bar{x}$	$s$	$\bar{x}$	$s$	$\bar{x}$	$s$	$\bar{x}$	$s$
1	108.7	25.2	17.2	4.4	15.7	0.6	4.9	1.7
2	135.6	22.6	14.6	3.8	12.8	1.0	5.7	1.4
3	102.2	16.0	14.1	3.0	14.3	0.9	4.4	1.3
4	123.3	21.6	21.4	8.9	15.7	0.5	3.9	2.2
5	119.8	21.1	21.5	3.9	15.6	0.4	4.1	1.8
6	115.4	17.8	17.8	6.4	15.5	0.4	3.6	2.1
7	120.5	21.4	23.4	11.0	15.8	0.7	3.5	2.1
8	119.4	14.8	17.8	6.2	15.5	0.4	3.1	1.7
9	125.5	22.8	22.2	9.3	15.4	0.6	4.1	2.3
10	125.1	21.6	24.6	10.5	16.4	1.2	3.5	1.6
11	119.5	17.0	18.9	4.9	16.3	1.2	3.8	1.7
12	119.8	22.9	21.6	6.0	16.0	1.1	3.9	2.1
13	121.0	22.7	22.9	7.4	16.3	1.3	4.0	1.7
14	136.5	17.6	19.8	5.0	14.0	1.5	5.1	1.3

**Table 3** Analyses of variance

Source	Height		Inflorescence size		Developmental stage		Saponin content	
	df	MS	df	MS	df	MS	df	MS
Lines	13	1 099.79***	13	118.53***	13	14.59***	13	7.48***
Years	4	15 343.94***	4	774.64***	4	12.96***	4	63.09***
Line × year	52	106.34**	52	39.01**	52	1.60***	52	3.17***
Reps w years	10	10.51	10	0.57	10	0.24	10	1.66
Error	108	62.53	81	23.83	109	0.15	127	1.60

\*  $P = 0.05 - 0.01$ ,  
 \*\*  $P = 0.01 - 0.001$ ,  
 \*\*\*  $P < 0.001$

**Table 4** Superiority and heterogeneity measures for the different characters, ranked from the optimum line *O*

Rank	Height			$P(het)_i$	$P_i$	Inflorescence size			$P(het)_i$	$P_i$
	Line	Mean (cm)	$P(o)_i^†$			Line	Mean (cm)	$P(o)_i$		
	<i>O</i>	101.40	0	0	0	<i>O</i>	26.96	0	0	0
1	3	102.15	28.05	44.16	14.43	10	24.56	13.86	12.15	5.19
2	1	108.69	603.18**	878.22***	296.28***	7	23.36	42.06	38.19	17.79
3	6	115.38	1771.32***	144.15	383.10***	13	22.89	50.46	57.42*	21.57
4	12	119.84	2774.61***	464.61***	647.85***	9	22.23	70.32	85.80**	31.23
5	5	119.85	2901.24***	544.62***	689.16***	5	21.45	95.49*	234.36***	65.97
6	13	121.00	2950.41***	481.68***	686.43***	12	21.61	104.13*	157.80***	52.38
7	11	119.46	2960.52***	97.29	611.55***	4	21.43	131.91*	55.17*	37.41
8	8	119.38	3080.94***	331.74***	682.53***	14	19.75	213.87**	173.37***	92.97
9	7	120.54	3172.83***	208.83**	676.32***	11	18.88	240.45**	430.53***	134.19
10	4	123.31	3842.22***	299.91***	828.42***	8	17.82	282.18***	519.69***	160.38*
11	10	125.14	4453.50***	543.78***	999.45***	6	17.82	310.47***	332.76***	128.64
12	9	125.50	4902.15***	1003.80***	828.42***	1	17.19	481.68***	429.96***	182.28*
13	2	135.64	8602.80***	485.97***	1817.73***	2	14.64	719.43***	556.74***	255.24**
14	14	136.51	10127.01***	76.32	2203.47***	3	14.14	826.89***	522.36***	269.85**
Error	MS		62.53					23.83		

Rank	Developmental stage			$P(het)_i$	$P_i$	Saponin content			$P(het)_i$	$P_i$
	Line	Mean	$P(o)_i$			Line	Mean	$P(o)_i$		
	<i>O</i>	16.40	0	0	0	<i>O</i>	2.15	0	0	0
1	10	16.36	0.25	0.18	0.09	8	3.07	0.15	0.22	0.09
2	13	16.32	0.41	0.30	0.15	10	3.53	2.70	1.14	0.78
3	11	16.31	0.76*	0.35	0.21	7	3.53	2.75	4.84*	1.50
4	12	16.00	2.56***	1.81***	0.87***	6	3.59	3.33	4.34*	1.53
5	1	15.71	4.42***	6.62***	2.22***	11	3.81	5.78	1.52	0.93
6	7	15.77	4.61***	12.38***	3.39***	4	3.94	5.89	6.91**	2.55
7	4	15.73	5.19***	9.01***	2.85***	12	3.94	7.68*	2.93	1.59
8	5	15.58	7.77***	7.51***	3.06***	13	3.98	8.33*	0.68	1.80
9	8	15.54	8.02***	9.39***	3.48***	9	4.11	10.55**	6.65**	3.45
10	9	15.43	9.11***	10.35***	3.90***	5	4.13	10.76**	20.18***	5.79**
11	6	15.46	9.34***	8.17***	3.51***	3	4.36	14.12**	2.23	4.77*
12	3	14.31	34.67***	16.02***	11.34***	1	4.93	29.76***	15.45***	10.14***
13	14	13.97	49.46***	1.88***	10.32***	14	5.05	33.90***	13.62***	7.26***
14	2	12.75	101.79***	6.23***	21.60***	2	5.75	59.64***	6.97**	11.73***
Error	MS		0.15					1.60		

\*\*\*, \*\*\*, \* Significantly different from the optimum value at  $P = 0.05 - 0.01$ ,  $P = 0.01 - 0.001$  and  $P < 0.001$ , respectively

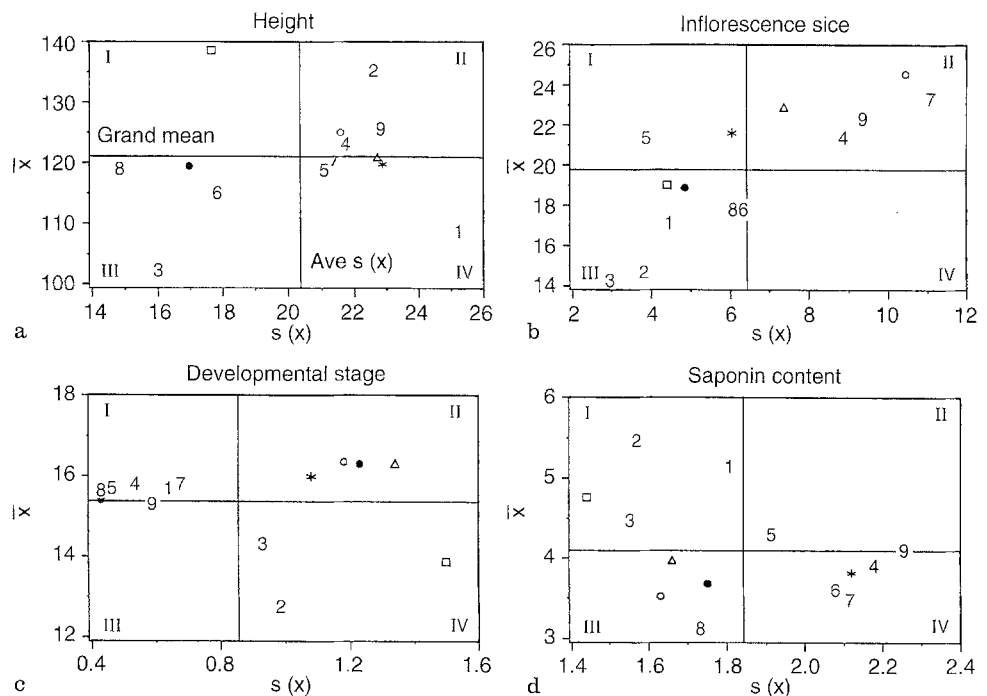
lines showing the most desirable expression in each year. The Lin and Binns' superiority measure  $P_i$  is calculated as a reference.

Short plants are preferred for seed production because they are supposedly drier at maturity and can therefore be harvested earlier. Line 3 is the shortest, not significantly different from the optimum. Two lines, 10 and 7, have an inflorescence size comparable to the optimum, and  $P(o)_i$  values homogeneous over years. These lines are therefore generally superior in all of the environments investigated. Early lines, that is those at a

high developmental stage, are preferred because of the considerable risk of seed loss at harvest due to adverse climatic conditions in northern Europe. With respect to development, lines 10 and 13 are neither significantly different from the optimum, nor do they exhibit significant heterogeneity. For saponin content, lines 8, 10 and 11 satisfy both criteria for the overall and heterogeneity  $P_i$  values.

Francis and Kannenberg (1978) demonstrated a significant correlation between mean yield and environmental variance,  $s_x^2$ , indicating that a variety that re-

**Fig. 1a-d** Means plotted against  $s_x$ , with sectors I-IV indicated. Symbols 1-9 are lines 1-9; ○, ■, ☆, △ and □ are lines 10-14, respectively



sponds to an improved environment has a large yield variance and hence may be presumed to have a high regression coefficient ( $1 + \beta_i$ ). This correlation was not confirmed by Becker (1981a) for cereals, and in this experiment it is only present for inflorescence size (Fig. 1). Average  $s_x$  and overall mean divide each graph in Fig. 1 into four sectors, with sector I having high mean and small  $s_x$ , sector II high mean and large  $s_x$ , sector III low mean and small  $s_x$  and sector IV low mean and large  $s_x$ . This approach is adapted from Francis and Kannenberg (1978), who used CV instead of  $s_x$ .

Table 5 combines the information supplied by the various stability parameters, and compares the average values for all lines in each of the four sectors of Fig. 1. Obviously, the number of lines in each sector will differ. Sector I contains tall plants with large inflorescences. Plants are stable with  $(1 + \beta_i) \approx 1.0$  and low residual deviations about the fitted regression line ( $s_d^2$ ). Lines in Sector III are short and have small inflorescences and a  $(1 + \beta_i) < 1.0$ , but for inflorescence size large deviations about the regression ( $s_d^2$ ) are apparent. Lines with the lowest  $P(o)_i$  values, that is closest to the optimum, occur for height and saponin content in sector III, where mean values are low. For inflorescence size and developmental stage, however, lowest  $P(o)_i$  values are found in sector II, where inflorescence size and developmental stage are high – that is the lines mature early.

## Discussion

Before deciding upon which method should be chosen for the evaluation of stability in quinoa, one has to ask how repeatable are these measure of stability when

genotypes are moved to other environments? Obviously, for stability parameters to have selection value they should be repeatable over environments. Becker (1981a) showed that the regression coefficient ( $1 + \beta_i$ ), environmental variance  $s_x^2$  and residual deviation  $s_d^2$  showed good agreement over 2 years in maize, but not in barley and oats. Fatunla and Frey (1976) found poor repeatability for oat genotypes when either a number of environments were assigned randomly to two sets, each including an identical set of genotypes, or when increasing- $N$  or increasing- $P$  environments were compared for the same genotypes.

Francis and Kannenberg (1978) detected a significant correlation between mean yield and environmental variance  $s_x^2$ , indicating that a variety which responds to an improved environment has a larger yield variance. This correlation was not detected by Becker (1981a), and in our investigation it was only present for inflorescence size. It may be presumed that a responsive variety with a large environmental variance would have a high regression coefficient. This was actually demonstrated for all characters recorded here. A similar relationship was found by Witcombe (1988) for yield in pearl millet, and by Becker (1981a,b) for cereals and maize. Lines identified as being stable by this method were often those selected by the combined use of regression slopes and residual deviations around the regressions. More information is supplied by this latter method because it tests whether a linear relation exists between the GE interaction and the environment, and how predictable this response is.

The superiority index  $P(o)_i$  offers certain advantages, because when using the optimum values in each environment as a standard, the necessity of having all con-

**Table 5** Comparison between stability parameters

Sector	Height		$1 + \beta_i$	$s_d^2$	$P(o)_i$	$P(het)_i$	$P_i$
	$\bar{x}$	$s_x$					
I	138.6	17.7	0.93	0.0	10 127.0	76.3	2203.5
II	128.0	22.2	1.11	47.8	5 450.2	583.4	1118.6
III	114.9	16.4	0.76	7.5	1 960.2	154.3	422.9
IV	118.0	22.7	1.11	19.9	2 480.5	515.6	586.3
Sector	Inflorescence size		$1 + \beta_i$	$s_d^2$	$P(o)_i$	$P(het)_i$	$P_i$
	$\bar{x}$	$s_x$					
I	21.5	5.0	0.95	0.0	99.8	196.1	59.2
II	22.9	9.4	1.63	0.9	61.7	49.8	22.6
III	17.1	4.7	0.46	4.9	439.3	423.6	174.8
IV	—	—	—	—	—	—	—
Sector	Developmental stage		$1 + \beta_i$	$s_d^2$	$P(o)_i$	$P(het)_i$	$P_i$
	$\bar{x}$	$s_x$					
I	15.6	0.5	0.24	0.2	6.7	8.7	3.2
II	16.3	1.2	1.83	0.2	1.0	0.7	0.3
III	—	—	—	—	—	—	—
IV	13.7	1.1	0.99	0.7	62.0	8.0	14.4
Sector	Saponin content		$1 + \beta_i$	$s_d^2$	$P(o)_i$	$P(het)_i$	$P_i$
	$\bar{x}$	$s_x$					
I	5.0	1.6	0.37	0.4	34.4	9.6	8.5
II	4.2	2.1	1.03	0.9	10.7	13.4	4.6
III	3.6	1.7	1.13	0.0	4.2	0.9	0.9
IV	3.7	2.1	1.87	0.0	4.9	4.8	1.8

trols in all environments is avoided. In this experiment, where the number of environments is insufficient for regression analysis, the superiority index is a useful alternative approach, as indeed it is also when the linear regression model fails.

It was stated by Pinthus (1973) that yield is strongly influenced by GE interaction, whereas maturity, height and disease resistance are not and hence selection for these latter characters could be based on a few nursery tests. The results presented here generally accord with this statement. Thus, although GE interactions were significant for all characters, for several of interest to the plant breeder, namely earliness, height and inflorescence size, some of the best lines track the optimum response. Saponin content apparently lacks this consistency, due mainly to an insufficiently sensitive measuring technique. It may be concluded, therefore, that for most of the characters recorded here, selection can be performed at an early stage of a breeding programme, when breeding material is scarce.

In quinoa, the ideal variety for seed production would have a consistently high seed yield and a low saponin content. In addition, it should be short, to facilitate mechanical harvesting, non-branching and uniformly early maturing. This latter attribute is important for North European conditions, where the risk of cold, humid weather, which will render harvesting difficult, increases in the autumn. Size, shape and compactness of the inflorescence may be important for the rate of maturation. A large, open inflorescence should

dry more quickly after rain and morning dew than a small, compact one, but it may also be more prone to seed scattering. Which lines fit this bill? Of course, no single line possesses all these attributes, but from Table 4 it can be seen that line 10 is early-maturing, and has a low saponin content and a large inflorescence. Line 3 is uniformly short in all five seasons. Assuming that the genes for these characters are inherited independently, selection amongst the progeny of a cross between lines 10 and 3 could result in recombinant material possessing many if not all these desirable attributes. For fodder production, on the other hand, tall, leafy, late-maturing material, with a high dry-matter yield and preferably low saponin content, is required. Recalculation of the overall and heterogeneity  $P_i$  values for height and developmental stage to take into account the opposite  $O$  value to that presented in Table 4 indicates that lines 14, 9 and 10 are tall, while line 2 is both tall and late and not significantly different from the optimum. They could, therefore, be suitable parents for such a breeding and selection programme. Since quinoa is predominantly an inbreeding species, breeding and selection programmes akin those commonly used in cereals could be adopted. Indeed, because of the masking effects of dominance, it might be appropriate to produce the recombinant inbred lines by single seed descent and defer selection to the  $F_6$  or even later generations, as suggested by Jinks and Pooni (1981).

Those genotypes whose overall mean does not depart significantly from the optimum and which do not have

significant heterogeneity can be recommended for a whole region. Both lines 3 and 10 come into this category; the former for height, the latter for several characters (Table 4). When the difference between the optimum and the best lines is significant, Lin and Binns (1988) suggest that several locally adapted varieties would be required, which can be identified by plotting cultivar and optimum means against the environmental mean. Varieties whose overall means are close to the optimum but which nevertheless have a significant heterogeneity  $P_i$  value should be examined in this context. The closeness of the observed value of the candidate variety to the optimum indicates areas of specific adaptation. This could be interesting, for example, in the poor environments of the high Andes, where the availability of nitrogen fertilizer is limited, or in Europe for use as a set-aside crop.

Low saponin content is likely to be a desirable attribute in many breeding programmes designed to produce commercial cultivars of quinoa, because they affect the palatability of seeds, making a dehulling process necessary before consumption. But saponins act as non-specific pest and disease repellants. Consequently, a breeding programme designed to reduce saponin content may have to be accompanied by a parallel programme for increased pest and disease resistance to replace that offered by the saponins. Alternatively, it might be possible to reduce saponin content to the point where it no longer has a negative effect on palatability, but still retains its pesticidal properties.

The topic of stability, particularly yield stability, is not new. It has long been a major preoccupation of plant breeders, and it has been a cherished ambition on their part to develop varieties with a uniformly high yield in all environments. But, as events have shown, this is almost certainly an impossible dream. Analyses of multi-environmental traits can, however, provide valuable information to breeders when choosing suitable material for their programmes. Indeed, what was sought in this investigation, was, with the aid of appropriately modified analytical techniques, the identification of material which would facilitate the breeding and development of quinoa cultivars, suitable for North European conditions. Steps in this direction have been taken, though further experimentation is still required.

**Acknowledgements** The authors wish to acknowledge Dr. E.L. Breese for reading and commenting upon the script, and Jordbrugsdirektoratet, the Danish Ministry of Agriculture, for financial support to the project.

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