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Quantitative phenotypical expression of three mutant genes in barley and the basis for defining an ideotype for Mediterranean environments

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Summary. Three mutants induced in the two-rowed barley variety Beka and their three binary recombinants have been used in an attempt to define an ideotype suitable for Mediterranean agroclimatic conditions. Physiological methods (classical plant growth analysis) together with the study of genotype × environment interaction for grain yield were used to characterize the genotypes. That characterization brought out the huge phenotypical variation produced by only three mutant genes, suggesting that single Mendelian genes may alone explain the quantitative variation, including grain yield, without the necessity of using the polygenic concept. The genotype best adapted to the environments studied is later in heading and has shorter straw and denser spikes than Beka; it also has higher inverse of leaf area rate and grain: leaf area ratio, a lower rate of leaf senescence, and a shorter grain filling period than the original variety.

Key words: Barley genetics – Quantitative gene expression – Ideotype – Mutants

Introduction

Donald (1968) based his new theoretical approach to the breeding of new varieties through the use of ideotypes mainly on a criticism of the classical ways to improve crop yields by "defect elimination" and "selection for yield." The former includes the correction of such imperfections of the varieties to be replaced as disease susceptibility, physical disadvantages (e.g., weak straw), low quality, etc., the latter an intent to improve yield without consideration of the whys or wherefores of the greater yield.

Donald (1968) proposed the breeding of model plants or ideotypes, which were defined as the ideal varieties to be grown in an optimal environment without any stress. This new approach should lead to the design of a plant (i) theoretically capable of greater production than the genotype it is to replace, and (ii) of such a phenotype as to offer a reasonable prospect of it being bred from available material.

While listing several of the characteristics known to influence yield positively, Donald also recommended that the ideotype variety must be subjected to "rigorous selection for yield." This last statement could mean: (i) that the newly added characteristics might act in an unpredictable manner; (ii) that the new approach is also empirical, such as that originally criticized; and (iii) that the genetic background of the variety could influence yield as much as the unknown combination of the model characteristics. Obviously, Donald never had an ecoagronomic concept with his ideotype, which was conceived for well-fertilized, well-watered lands such as the areas of northern Europe. Therefore, when dealing with environmental conditions such as the ones prevailing in the Mediterranean area, which are far from ideal, a different kind of approach should be used.

We have tried here to lay the foundations for the definition of such a barley ideotype through an experimental approach based on the knowledge of the effect of various physiological parameters, derived from growth analysis techniques, yield value, and stability. This approach is, however, not new, because already in 1966, Mac Key wrote about the necessity of taking into account physiological parameters when defining the most efficient type of plant to be bred. At that time, the term "ideotype" was not yet coined.

The originality of our study lies, however, not in its ecophysiological approach alone, because cooperation

Table 1. Description of the ten environments used

Trial no.	Year	Location	Coordinates	Altitude (m)	Annual rainfall (mm)	Soil fertility	Site yield (kg/ha)
1	1984	Alcala del Rio, Sevilla	37°30′N 6°00′W	12	440	Very high	8,932
2	1985	Alcala del Rio, Sevilla	37°30′N 6°00′W	12	624	Very high	5,894
3	1986	Alcala del Rio, Sevilla	37°30′N 6°00′W	12	394	Very high	6,043
4	1987	Domingo Perez, Granada	37°30′N 3°30′W	900	761	High	4,442
5	1987	Colomera, Granada	37°23′N 3°42′W	600	400	Low	3,837
6	1987	Alcala del Rio, Sevilla	37°30′N 6°00′W	12	724	Very high	5,736
7	1988	Domingo Perez, Granada	37°30′N 3°30′W	900	432	High	3,595
8	1988	Colomera, Granada	37°23′N 3°42′W	600	370	Low	7,356
9	1988	Tembleque, Toledo	39°42′N 3°30′W	720	353	Low	3,356
10	1988	Villarramiel, Palencia	42°03′N 4°55′W	780	420	Medium	3,059

between plant physiologists and breeders is not new, but in the use of *true near-isogenic lines*, to avoid the misleading results derived from the effect of the genetic background on plant adaptation and yield. This criticism might be relevant to studies that use an array of different genotypes of wide-spread geographic origin to study such a problem, without really knowing the effect of genotype × environment interactions arising from the different genetic backgrounds used.

To overcome the problem pointed out by Donald (1968) regarding the uncertainty of the adaptation of the ideotype to the desired environment, we have used Beka, a barley variety well adapted to the Spanish growing conditions, and near-isogenic lines that have been bred, firstly, through inducing mutations in Beka, by selecting mutants with strikingly different plant architectures and phenological characteristics but good adaptation to our conditions and, secondly, by breeding recombinants from these mutants.

Most of the characters studied are included in Rasmusson's list (1987) as traits with the potential for increasing yield by ideotype breeding in small grains.

Classical plant growth analysis (Kvet et al. 1971; Evans 1972; Warren Wilson 1981) envisages the growth of crop plants (biomass accumulation or crop dry weight, CDW) as a consequence of both their capacity for light interception (leaf area index, LAI) and the activity of their photosynthetic organs (production of dry matter per unit of leaf area measured as the inverse of the leaf area rate, 1/LAR). These factors depend directly upon the basic physiological processes of photosynthesis, respiration, and photosynthate translocation, and may be used to investigate the influence of genetic and environmental factors on crop growth and grain yield and on their components.

The photosynthates needed for filling the barley kernels come from two different sources: (a) the carbohydrates stored during the vegetative phase in shoots and leaves, and (b) the assimilates synthesized after ear emergence (Watson et al. 1963; Evans and Wardlaw 1976). The assimilation rate after ear emergence depends on the duration of photosynthesis itself (leaf area duration, LAD) and on its efficiency in producing materials for filling the kernels (G) (Thorne 1974).

Materials and methods

Plant material

Beka, the parent variety used, was chosen for its extremely good adaptation to the arid Mediterranean conditions prevailing across most of the barley area in Spain, and it has been widely grown here since its release in 1965.

Five hundred grams of dry seeds of Beka were irradiated with gamma rays (20 krad) and the three mutants used in this study were selected in the M_2, as described by Molina-Cano (1982). Three morphologically very different mutants (genes 1, 2, and 3) were crossed in all possible combinations, excluding reciprocals, and the three binary recombinants were then selected in F_2 and purified in F_3. These are named recombinants 12, 13, and 23. All mutant and recombinant genotypes are described in Tables 2–6 and Figs. 1–3.

All three mutants were recessive (Molina-Cano 1982; F. Roca de Togores, unpublished results). Gene 3 was identified as a mutation at locus *ert-d*, as described by Persson and Hagberg (1969) (Molina-Cano 1982)

Field methods

Ten yield trials were carried out from 1984 to 1988 under rainfed conditions. The sites (Table 1) were distributed across the most important barley-producing regions of Spain, thus constituting a good sample of the different types of Mediterranean environments prevailing in the country. At Alcalá del Río (Sevilla), Colomera (Granada), and Tembleque (Toledo) there are sharp rises in temperatures accompanied by a water deficit during grain filling, whereas Domingo Pérez (Granada) provides excellent conditions during the later part of the growing season. The climate at Villarramiel (Palencia) is intermediate between these two types.

A trial was laid out at every environment consisting of a randomized block design with four replications. Plot size was 12.6 m², and each plot consisted of eight rows, 11 m long and 15 cm apart in Alcalá del Río (1985 and 1986) and of six rows, 11 m long and 20 cm apart, at the remaining sites. Physiological

Table 2. Average grain yield per plant and its components over four environments (Domingo Pérez and Colomera, 1987 and 1988)

Line	Gene(s)	Grain yield/ plant (g)	Spikes/plant	Kernels/spike	Thousand-kernel weight (g)	Spikes/m^2
Beka	Wild type	2.48 a	2.51 ab	22.78 b	42.94 a	620 a
1	1	2.00 d	2.58 a	18.24 d	41.74 bc	629 a
2	2	2.28 bc	2.40 b	23.16 b	41.03 c	596 a
3	3	2.47 a	2.52 ab	23.05 b	42.60 ab	619 a
12	1 & 2	2.02 d	2.53 ab	19.92 c	39.64 d	615 a
13	1 & 3	2.19 c	2.58 a	19.78 c	42.86 a	603 a
23	2 & 3	2.34 ab	2.39 b	24.69 a	39.47 d	586 a

Note: means followed by the same letter within each column do not differ significantly at the type I error ($\alpha = 0.05$) using the LSD test after analysis of variance

Table 3. Growth indexes at anthesis and maturity. Mean values of four environments (Domingo Perez and Colomera, 1987 and 1988)

Line	Anthesis			Maturity	
	CDW	LAI	1/LAR	LAD	G
Beka	573 a	3.77 a	156 d	10.45 a	250 g
1	371 d	1.92 c	213 ab	5.25 c	353 ab
2	488 c	2.99 b	169 cd	8.27 b	370 ab
3	653 a	3.19 b	202 b	8.98 b	364 ab
12	395 d	1.81 c	222 a	5.14 c	433 a
13	427 cd	2.02 c	216 ab	5.41 c	423 a
23	603 a	3.42 ab	178 c	8.99 b	310 bc

Note: means followed by the same letter within each column do not differ significantly at the type I error ($\alpha = 0.05$) using the LSD test after analysis of variance

measurements were taken at Domingo Pérez and Colomera in 1987 and 1988.

Physiological methods

Plants growing in 0.5 m of row per plot were collected at intervals of about 15 days during the principal developmental stages until ripening (Large 1954). Five representative plants per plot were used in the laboratory to estimate the mean of the following original variables: (a) total above-ground dry matter (W) and separate dry weight value of leaves, tillers, and ears (after drying at 70–80 °C to constant weight); (b) leaf lamina area (A) by using a photoelectronic planimeter; and (c) number of plants per unit area (N). From these data, the values of each growth index were calculated as follows:

CDW = LAI.1/LAR (Warren Wilson 1981)
NW = NA.W/A (Warren Wilson 1981)
LAD = (LAI anthesis + LAI maturity)/2 (time anthesis to maturity) (Hunt 1982)
G = Grain yield/LAD (Watson et al. 1963)

Statistical methods

Two multivariate methods have been used in order to clarify and interpret the complex data collected, i.e., the unweighted pair-group method using centroids (UPGMC) clustering, and principal component analysis (PCA) (Sneath and Sokal 1973). These methods were used with success by the senior author to classify barley cultivars (Molina-Cano 1976; Molina-Cano and Elena-Roselló 1978).

To assess genotype × environment interaction, two methods were used: the standard regression of genotype yield on site mean yield (Finlay and Wilkinson 1963) and a non-parametric rank method (Ketata et al. 1989).

All statistical analyses were carried out on a DEC-microVAX computer using standard SAS procedures (SAS 1988).

Results

Yield per plant variation and growth analysis

The comparison between the mean values of yield per plant (Table 2) shows that Beka and line 3 yield significantly more than the other genotypes, probably due to their well-balanced yield components. There is also a group of genotypes with intermediate yield level (lines 23 and 2) due to an imbalance in thousand-kernel weight. The lower yielding lines are the very early and shorter genotypes, all carrying gene 1; all of them have a very reduced number of kernels per spike and lines 1 and 12 have a low kernel weight.

The data obtained from classical growth analysis (Table 3) indicated a close relationship between yield per plant and both crop dry weight at anthesis, CDW ($r = 0.93$; $\alpha \leq 0.01$) (in turn depending on LAI, $r = 0.89$; $\alpha \leq 0.01$), as well as LAD from anthesis to maturity ($r = 0.93$; $\alpha \leq 0.01$).

Variation patterns of LAI and LAD among genotypes are similar to those of yield. Thus, the very early, low-yielding genotypes also have the lowest LAI and LAD values (Table 3). A study of the components of these indexes (Table 4) shows that this variation was mainly caused by changes in leaf size and, to a lesser extent, in the number of leaves per plant.

Genotype × environment interaction for grain yield

Table 5 shows the mean yield of each genotype over the ten testing sites and the stability estimates for the regression-based method. The stability study is completed with Fig. 1, which shows the results of the genotypic rank analyses and Fig. 2a, which is the UPGMC phenogram

Table 4. Components of the growth indexes LAI and LAD at anthesis and maturity. Mean values of four invironments (Domingo Perez and Colomera, 1987 and 1988)

Line	Anthesis				Maturity			
	Leaves/ plant	Leaf area (cm^2)	Plant area (cm^2)	Plants/m^2	Leaves/ plant	Leaf area (cm^2)	Plant area (cm^2)	Plants/m^2
Beka	15.2 a	9.7 a	181.3 a	251 a	5.8 a	4.9 a	31 a	237 a
1	13.4 bc	6.2 c	105.4 c	228 a	4.6 b	2.7 c	12 c	238 a
2	13.7 abc	8.7 b	146.8 b	243 a	6.2 a	5.5 a	37 a	234 a
3	14.4 ab	10.2 a	178.8 a	234 a	5.6 ab	5.4 a	32 a	228 a
12	12.5 c	6.2 c	93.5 c	245 a	6.0 a	3.2 bc	21 b	242 a
13	13.5 bc	6.5 c	109.8 c	236 a	4.6 b	3.7 b	18 bc	239 a
23	13.7 abc	10.4 a	171.8 a	240 a	6.3 a	5.3 a	34 a	246 a

Note: means followed by the same letter within each column do not differ significantly at the type I error ($\alpha = 0.05$) using the LSD test after analysis of variance

Table 5. Genotype × environment interaction for grain yield: average genotypic yield regressed on environmental (site × year) mean yield

Line	Average yield (kg/ha)	Regression estimates		
		a	b	r^2
Beka	5,419 a	371	0.97 a	0.95
1	4,637 b	−700	1.02 a	0.92
2	5,641 a	239	1.03 a	0.97
3	5,458 a	1,300	0.80 b	0.83
12	4,829 b	−532	1.03 a	0.87
13	5,113 ab	−426	1.06 a	0.94
23	5,503 a	244	1.01 a	0.95

Note: means followed by the same letter within each column do not differ significant at the type I error ($\alpha = 0.05$) using the LSD test after analysis of variance
Regression line: $y = a + bx$; r^2 = coefficient of determination

obtained by using the yield data of each genotype at each environment as classifying characteristics.

Regression analyses reveal that all lines, except no. 3, show linear slopes around unity. That is, their yields increase roughly at the same rate as the environment improves. Line 3 exhibits smaller slope than 1, which suggests its superiority over the others in the poorer environments. The original genotype, Beka, and the lines carrying gene 2 perform well over all the environments, particularly the higher yielding ones. Lines carrying gene 1 always yield less than the rest, irrespective of the environmental indexes.

The results of rank analysis (Fig. 1) suggest that genotype 2 is the superior one, showing as it does the lowest mean rank and standard deviation. Genotypes 3 and 23, however, although also manifesting low mean rank, have a high standard deviation, indicating inconsistency to environmental changes. The mother variety, Beka, exhibits an intermediate behavior.

Genotypes carrying gene 1 always display either high rank and standard deviation (recombinants 12 and 13) or low variation for high rank (line 1). In either case, they perform very poorly.

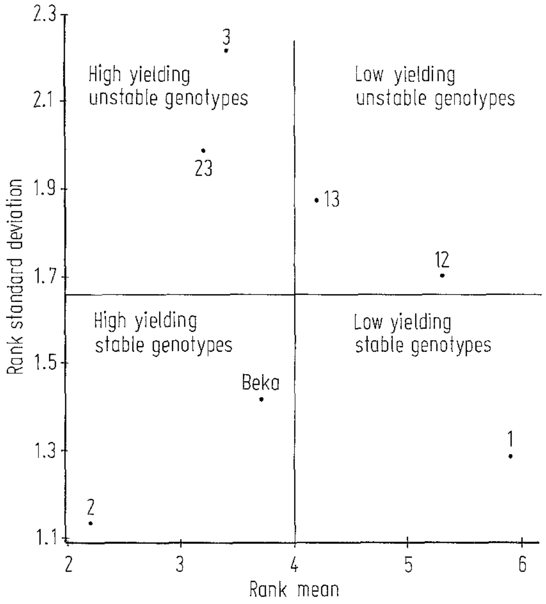

Fig. 1. Grain yield stability of Beka and its derivatives over ten environments studied with the aid of nonparametric rank analysis. Rank means on the X axis and their standard deviations on the Y axis. The four regions established are only orientative

The dendrogram of Fig. 2a shows two main clusters: one made up of genotypes carrying gene 1, characterized by low yield in all the environments, and the rest showing good yielding performance.

The data support the idea of an epistatic effect of gene 1 on genes 2 and 3. When gene 1 is present in a line its yielding ability is poor, irrespective of whether another gene is present. This fact is also sustained by the growth analysis and morphophysiological data presented elsewhere in this paper. Moreover, the morphophysiological traits associated with gene 1, i.e., small leaf area at anthesis and extreme earliness, should be considered as detrimental to achieving high yields.

Table 6. Morphophysiological description of the genotypes studied over four environments (Domingo Perez and Colomera, 1987 and 1988)

Line	Morphophysiological characters[a]								
	1	2	3	4	5	6	7	8	9
Beka	15.2 a	5.8 a	9.7 a	4.9 a	70.4	76.9 a	131 b	31 a	2.8 c
1	13.4 bc	4.6 b	6.2 c	2.7 c	71.3	60.4 bc	124 c	31 a	2.9 c
2	13.7 abc	6.2 a	8.7 b	5.5 a	68.5	63.7 b	134 b	30 ab	4.4 a
3	14.4 ab	5.6 ab	10.2 a	5.4 a	70.3	70.9 a	135 a	29 b	3.6 b
12	12.5 c	6.0 a	6.2 c	3.2 bc	72.1	53.1 d	125 c	31 a	4.4 a
13	13.5 bc	4.6 b	6.5 c	3.7 b	72.3	59.7 c	128 b	29 b	3.5 b
23	13.7 abc	6.3 a	10.4 a	5.3 a	68.2	63.1 bc	136 a	29 b	4.3 a

[a] List of characters: 1: No. of leaves/plant at anthesis; 2: No. of leaves/plant at maturiy; 3: Leaf area at anthesis (cm^2); 4: Leaf area at maturity (cm^2); 5: Leaf angle (degrees); 6: Length of the main shoot (cm); 7: Days emergence – anthesis; 8: Days anthesis – maturity; 9: Spike density (no. kernels/cm of rachis)

Note: means followed by the same letter within each column do not differ significantly at the type I error ($\alpha = 0.05$) using the LSD test after analysis of variance

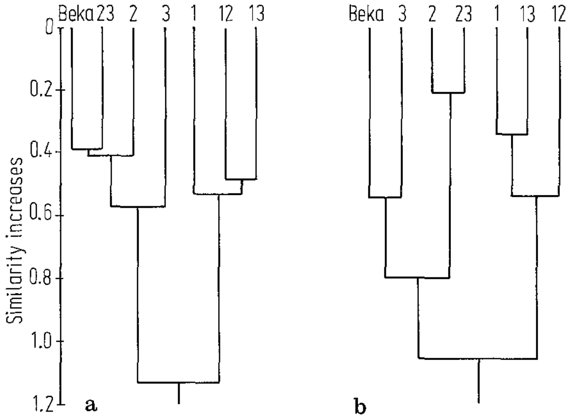

Fig. 2a and b. Clustering of the genotypes with UPGMC, calculated from grain yield data at each of ten environments (**a**), from the nine morphophysiological traits of Table 6 (**b**). Note the close resemblance between the clusters formed in both phenograms

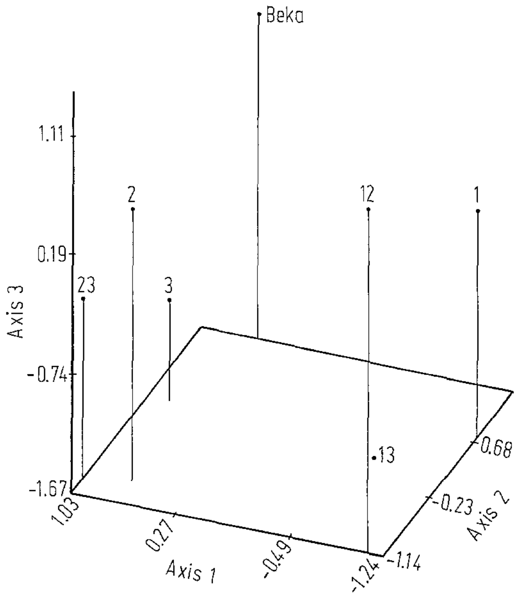

Fig. 3. Three-dimensional grouping of the genotypes obtained from principal component analysis of the morphophysiological data of Table 6. These three first axes accounted for more than 97% of total variance. Axis 1 is related to gene 1, whereas axes 2 and 3 are related to genes 2 and 3, respectively

Morphophysiological analysis

The data used in this analysis (Table 6) encompass morphological characteristics related to canopy structure: the number of leaves per plant and leaf area at anthesis and maturity, leaf angle and length of the main shoot; and one characteristic related to spike morphology: spike density. Furthermore, physiological characteristics related to life cycle, such as days from emergence to anthesis and the length of the grain-filling period, are also included.

It can be seen in Table 6 that there are statistically significant differences among genotypes for all studied characteristics, except leaf angle. This demonstrates the great phenotypical variation existing among genotypes, in spite of their close genetic similarity. The phenetic relationships existing among the studied genotypes (Table 6) are shown more clearly by UPGMC clustering (Fig. 2b) and principal component analysis (Fig. 3).

In Fig. 2b as in Fig. 2a, two main clusters are displayed. The first brings together all the genotypes carring gene 1. The other, made up of the rest of the lines, is composed of two subclusters, one with all lines carrying gene 2, and the other one with Beka and genotype 3, which joint at a lower level of similarity. It is interesting now to note the close correspondence existing between Fig. 2a and 2b, although they were produced from two completely different sets of characteristics. Their most striking resemblance is a consequence of the overall effect of gene 1, both on yield in different environments and on the general appearance of the canopy and life cycle.

Before discussing Fig. 3, we should mention that the first three principal components account for more than 97% of the total variance, thus explaining most of the total variation underlying the data in Table 6. From this table and Fig. 3, plus the character loadings on the first three principal components (not given here), we can extract the following information.

(i) The genotypes group on the space determined by the first three axes following roughly the same pattern as in the two preceding phenograms (Fig. 2a and 2b), i.e., all lines carrying gene 1 cluster together, as do the two lines with gene 2. Line 3 is in between Beka and the gene 2 cluster, but well apart from the gene 1 cluster.

(ii) The first principal component is related to gene 1, as the characteristics possessing the higher loadings on it are governed by this gene. Consequently, the separation of lines carrying this gene from the rest is made along this axis. These lines show a smaller leaf area at anthesis and are much earlier in heading than the others.

(iii) The second principal component is related in a similar fashion to gene 2. These lines have denser spikes and more leaves at maturity than the other genotypes.

(iv) The third principal component is related to gene 3, mainly through the length of the grain-filling period; genotypes 3, 13, and 23 need a shorter period for filling the kernels. They all show the smallest coordinates along the third axis.

The data presented so far disclose the following epistatic relationships: (i) there is an epistatic effect of gene 1 on genes 2 and 3; (ii) gene 2 is also epistatic on gene 3.

Discussion

A close relationship has been shown between the three mutant genes involved and grain yield and overall adaptation to the environment, via morphophysiological modifications of the phenotype. Thus, the genotypes carrying gene 1 have smaller and fewer leaves at anthesis and maturity, as well as lower leaf area duration. This is very disadvantageous to the very early genotypes, which had a smaller "source capacity" in comparison with Beka. In addition, this drawback is enhanced as these genotypes also have the shortest culms, the organs mainly involved in the accumulation of carbohydrate reserves at anthesis. The importance of the last factor has been repeatedly pointed out for environments with water deficits during grain filling (Austin et al. 1980; Lawlor et al. 1981; Ramos et al. 1985, 1989). Furthermore, the earliness and reduced LAD of the very early genotypes result, in this kind of environment, in a lower photosynthetic capacity and opportunity for assimilate translocation to the growing kernels, thus setting limits to grain yield.

All the huge phenotypic variation recorded is probably the effect of only three recessive Mendelian genes, segregating 3:1 in F_2 (Molina-Cano 1982; F. Roca de Togores, unpublished results). Thus, with this reduced group of genes we may explain quantitative variation, which conventionally could only have been studied with the use of the polygenic theory and the aid of quantitative genetics. Although the quantitative effect of major genes has been shown many times in barley (e.g., Persson and Hagberg 1969), Molina-Cano et al. (1989) have recently presented evidence for single mutations that produce a broad mosaic of phenotypic expression, including such typical quantitative characteristics as grain yield and malting quality (malt extract yield, among other things), together with others of well-documented oligogenic and monogenic inheritance, such as β-glucan content and germination speed.

All this evidence supports the possibility of genetically transforming barley by the direct transfer of single genes that control grain yield and other quantitative traits, provided the adequate biochemical markers are used.

The general analysis of the data presented allows us to outline the identity of an ideotype suitable for Mediterranean climatic conditions, by comparing the advantages of the most successful mutant with the mother variety, Beka. The negative traits shown by the inferior variants have also been revealed.

Overall, genotype 2 gives the highest and most stable grain yield over environments. Its differences from Beka are: lower rate of leaf senescence; higher activity of the photosynthetic organs at anthesis (1/LAR) and efficiency in producing materials to fill in the kernels (G); shorter straw; slightly later heading; shorter grain filling period; denser spike.

When genes 2 and 3 act jointly, both grain yield and its stability diminish, so that recombinant 23 is closer to genotype 3 (Fig. 1). This lower yield stability is presumably due to a later heading and a shorter grain-filling period of genotypes 3 and 23 as compared to 2. It might also be hypothesized that yield instability caused by gene 3, an *erectoides* mutant, may be alternatively due to a shallow root system, as was the case presented by Mac Key (1987) when studying a collection of this type of mutants. This hypothesis need however to be tested.

The unfavorable effects brough about by gene 1, as compared to Beka, might be summarized as follows: fewer and smaller leaves at anthesis and maturity, enhanced leaf senescence, culm too short, heading too early.

Before concluding, it is interesting to recall again the demonstrated cause and effect relationships among: (a) a punctual genetic change exemplified by three gene mutations; (b) drastic modifications in plant architecture and physiological behavior of the mutant genotypes; and finally (c) severe alteration of the agronomical performance of the studied lines, as summarized by grain yield. In Fig. 2a and 2b the relationship between gene mutation, morphophysiological changes, and grain yield modification is clearly shown by the parallelism among the clusters formed with both sets of characteristics.

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References

Austin RB, Morgan CL, Ford MA, Blackwell RD (1980) Contributions to grain yield from pre-anthesis assimilation in tall and dwarf barley phenotypes in two contrasting seasons. Ann Bot 45:309–319

Donald CM (1968) The breeding of Crop ideotypes. Euphytica 17:385–403

Evans GC (1972) The quantitative analysis of plant growth. Blackwell, Oxford

Evans LT, Wardlaw IF (1976) Aspects of the comparative physiology of grain yield in cereals. Adv Agron 28:301–359

Finlay KW, Wilkinson GN (1963) The analysis of adaptation in a plant breeding program. Aust J Agric Res 14:742–754

Hunt R (1982) Plant growth curves. The functional approach to plant growth analysis. Arnold, London

Ketata H, Yau SK, Nachit M (1989) Relative consistency performance across environments. Int Symp Physiol Breed Winter Cereals for Stressed Mediterranean Environ, Montpellier, July 3–6, 1989 (in press)

Kvet J, Ondok JP, Necas J, Jarvis PG (1971) Methods of growth analysis. In: Sestak Z, Catsky J, Jarvis PG (eds) Plant photosynthetic production. Manuals of methods. Dr. W. Junk, The Hague, pp 343–391

Large EC (1954) Growth stages in cereals. Illustration of the Feekes scale. Plant Pathol 3:128–129

Lawlor DW, Day W, Johnston AE, Legg BJ, Parkinson KJ (1981) Growth of spring barley under drought: crop development, photosynthesis, dry matter accumulation, and nutrient content. J Agric Sci 96:167–187

Mac Key J (1966) The wheat plant as a model in adaptation to high productivity under different environments. In: 5th Yugoslav Symp Res Wheat, Novi Sad, 1966. Savrem poljiprivr 14:37–48

Mac Key J (1987) Shoot and root interrelation in barley. In: Yasuda S, Konishi T (eds) Barley genetics V. Proc 5th Barley Genet Symp. Sankyo Press, Okayama, pp 461–464

Molina-Cano JL (1976) A numerical classification of some European barley cultivars. Z Pflanzenzuecht 76:320–333

Molina-Cano JL (1982) Genetic, agronomic, and malting characteristics of a new erectoides mutant induced in barley. Z Pflanzenzuecht 88:34–42

Molina-Cano JL, Elena-Rosello JM (1978) A further contribution to the classification of barley cultivars: use of numerical taxonomy and biochemical methods. Seed Sci Technol 6:593–615

Molina-Cano JL, Roca de Togores F, Royo C, Pérez A (1989) Fast-germinating low β-glucan mutants induced in barley with improved malting quality and yield. Theor Appl Genet 78:748–754

Persson G, Hagberg A (1969) Induced variation in a quantitative character in barley. Morphology and cytogenetics of erectoides mutants. Hereditas 61:115–178

Ramos JM, Garcia del Moral L, Recalde L (1985) Vegetative growth of winter barley in relation to environmental conditions and grain yield. J Agric Sci 104:413–419

Ramos JM, Garcia del Moral LF, Molina-Cano JL, Salamanca P, Roca de Togores F (1989) Effects of an early application of sulphur and ethephon as foliar spray on the growth and yield of spring barley in a Mediterranean environment. J Agron Crop Sci 163:129–137

Rasmusson DC (1987) An evaluation of ideotype breeding. Crop Sci 27:1140–1146

SAS Institute, Inc. (1988) SAS language guide, Release 6.03 Edition, Cary/NC

Sneath PHA, Sokal RR (1973) Numerical taxonomy. Freeman, San Francisco

Thorne GN (1974) Physiology of grain yield of wheat and barley. Rothamsted Exp Stn Rep 1973, part 2, pp 5–25

Warren Wilson J (1981) Analysis of growth, photosynthesis, and light interception for single plants and stands. Ann Bot 48:507–512

Watson DJ, Thorne GN, French SAW (1963) Analysis of growth and yield of winter and spring wheats. Ann Bot 10:41–72