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Biometrical Analyses of Some Economically Important Characters in *Antirrhinum majus*

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Summary. The experiment described in this paper was designed to measure some of the genotype-environment interactions in *Antirrhinum majus* and the emphasis has been upon characters which are of economic importance. - Seven F_1 hybrids were grown in 27 different environmental conditions, consisting of 3 levels of nitrogen and 9 sowing dates. Analysis of variance followed by regression analysis and the partitioning of the variation into its genetic, environmental and interacting components were employed. - The practical applications of these methods by the grower and plant breeder, are discussed.

Introduction

The maintenance of strict schedules in the production of glasshouse ornamental flowering plants demands a high degree of prediction of quality and flowering time. This precise control requires a knowledge of the responses of varieties to the environmental variables encountered by the crop. A great deal of information exists for *Chrysanthemum* and other established ornamentals but there is only limited knowledge of the responses of *Antirrhinum* grown under English conditions. Studies of several varieties of *Antirrhinum* grown in controlled environments have demonstrated differences in their responses to light intensity (Hedley 1974a and b, and Hedley and Harvey 1975), daylength (Hedley 1974a and b) and temperature (Edwards 1974) and a preliminary study has indicated variation in the response to nitrogen level (Arthur and Hedley, in press).

When the effects of temperature and nitrogen were examined under controlled and constant conditions, genotypes were shown to vary in their response to environment, for many of the characters studied (Arthur and Hedley, unpublished data). When these genotype-environment interactions are present the relative performance of a variety as compared to the other varieties will, by definition, depend on the environment, and the varietal performance in different conditions cannot be predicted. These interactions can be analysed using statistical techniques where the mean of the responses of a number of genotypes in a range of environments is used to assess the overall effect of each of the environments used. The end result is likely to be a linear response of the genotypes' performance to the ranked changes in the environmental values (Finlay and Wilkinson 1963).

Experiments designed to measure the degree of genotype-environment interaction using characters likely to be of horticultural and economic value in Antirrhinums are reported.

Materials and Methods

Nine consecutive sowings of four early (Montezuma, Navajo, Pink Ice and Snowman)[1] and three late (Bronze Rocket, Orchid Rocket and White Rocket)[1] flowering F1 hybrid varieties of *Antirrhinum* were made at two weekly intervals, commencing on 20.8.74. From each sowing, ten plants of each variety were pricked into 9 cm diameter pots containing John Innes compost. Three initial levels of nitrogen were employed: the standard level in the JI1 compost, and half and double this concentration. Hence the effect of 27 environmental conditions on seven genotypes was examined. The plants were randomised on a single plant basis and grown in a greenhouse in which a minimum day and night temperature of 5°C was maintained throughout.

A number of economically important plant characters were recorded at the anthesis of the first flower: Budding time - the time from sowing to the appearance of the first macroscopic flower buds, measured in days; time from budding to flowering, where flowering is the period from sowing to the opening of the first flower, measured in days; Leaf number - the total number of leaves at flowering; Number of flowers per spike, including flower buds; Density of the flower spike - number of flowers per spike/length of the spike; Total height - length from cotyledonary node to the tip of the flower spike, measured in mms; Length of the flower spike/total height; Branching index - number of branches longer than 1 cm/leaf number.

* On postdoctoral leave from the Hebrew University of Jerusalem.

Table 1. Degrees of freedom and mean squares derived from the analyses of variance

	d.f.	Budding time	Time from budding to flowering	Leaf number	No. of flowers per spike	Density of flower spike	Total height	Length of flower spike × 10^{-4}/ total height	Branching index × 10^{-3}
Varieties (VAR)	6	8023.93***	960.03***	1348.39***	139.81***	395.67***	354459.44***	99.33***	516.55***
Environments (EN)	26	1578.23***	521.40***	692.41***	101.75***	42.32***	112647.22***	14.42***	10.98***
VAR × EN	156	234.69***	36.87***	42.14***	6.85***	3.14***	5599.26***	0.84***	3.71***
Heterogeneity of regression	6	642.37***	714.16***	322.22***	17.00***	16.00***	22943.09***	5.83***	17.63***
Residual	150	218.39***	9.78***	30.94***	6.45***	2.63*	4905.59***	0.64***	3.15***
Error (based on harmonic mean)	1398	12.77	3.69	5.12	3.27	2.11	2606.74	0.49	1.70
% Linear proportion		75.38	99.15	92.47	81.19	96.39	89.84	97.27	91.66

(* 5-1%P, ** 1-0.5%P, *** <0.5%P).

Analysis of variance

The random model situation was used for the statistical analyses as the factors involved in this experiment have been considered as random effects. The error terms were derived as the total of the sum of squares of the individual plants of each cultivar at each sowing and each nitrogen level. The error mean square was corrected for missing plants by dividing it by the harmonic mean.

Regression analysis

The application of the linear regression technique to the analysis of genotype-environment interactions in plants other than grasses has been dealt with in detail elsewhere (Snoad and Arthur 1974, 1976; Arthur and Hedley in press.) For the purposes of this paper, we have interpreted the slopes of the regression lines as measurements of stability of degree of response. The seven regression lines allow comparison of each variety with the average of the seven. Thus, regressions of unit slope have an average degree of response, those greater than one, above average, and *vice versa*.

[1] Montezuma - from D.R. Colegrave Seeds Ltd., England. Navajo, Pink Ice, Snowman, Bronze Rocket, Orchid Rocket and White Rocket from Suttons Seeds Ltd., England.

Results and Discussion

Mean squares values derived in the analyses of variance of eight economically important characters are given in Table 1. A statistically significant interaction between genotypes and environments was found in all instances and the main effects of genotypes and environments show high significance when tested against the significant interaction mean square. As a result, no immediate generalisation can be made on the relative performance of each cultivar over the range of the tested environments.

The large number of treatments, varieties and replications, and the extremely high degrees of freedom for the error term (Table 1) enable us to detect even minute differences as being statistically significant. It was important therefore to examine the values of the variance components, according to the random model used in these analyses, so as to determine the relative importance of the factors involved (Table 2). The computation showed that in five of the measured characters (number of flowers per spike,

Table 2. Values and percentages for the components of variation derived from the analyses of variance using the random model

Character	Value				%			
	σ^2E	σ^2VAR×EN	σ^2EN	σ^2VAR	σ^2E	σ^2VAR×EN	σ^2EN	σ^2VAR
Budding time	12.77	29.86	25.83	38.82	11.90	27.83	24.08	36.19
Time from budding to flowering	3.69	4.46	9.31	4.60	16.73	20.22	42.20	20.85
Leaf number	5.12	4.98	12.50	6.51	17.58	17.11	42.94	22.36
No. flowers per spike	3.27	0.48	1.82	0.66	52.40	7.73	29.25	10.62
Density of flower spike	2.11×10^{-4}	0.14×10^{-4}	0.72×10^{-5}	1.96×10^{-4}	49.28	3.27	1.68	45.77
Total height	2606.74	402.69	2057.83	1738.67	38.30	5.92	30.24	25.55
Length of flower spike/total height	4.85×10^{-5}	0.48×10^{-5}	2.61×10^{-5}	4.91×10^{-5}	37.76	3.71	20.32	38.21
Branching index	16.99×10^{-4}	2.70×10^{-4}	1.40×10^{-4}	25.56×10^{-4}	36.42	5.79	3.00	54.79

Table 3. Mean values for the seven varieties calculated over the 27 environments

Variety*	Budding time	Time from budding to flowering	Leaf number	No. of flowers per spike	Density of flower spike	Total height	Length of flower spike/ total height	Branching index
Pink Ice	139.6** d	41.4 a	47.2 d	24.3 ab	0.18 bc	1105.1 bc	0.12 bc	0.98 a
Montezuma	146.8 cd	38.9 ab	57.0 bc	25.6 a	0.17 bcd	1147.2 abc	0.13 ab	0.92 a
Snowman	154.8 c	36.5 ab	53.7 cd	25.5 a	0.25 a	1005.5 cd	0.11 cd	0.92 a
Navajo	166.3 b	32.1 bc	59.5 bc	22.8 ab	0.20 b	1274.9 a	0.09 d	0.96 a
Orchid Rocket	174.0 ab	29.0 cd	60.6 b	22.6 ab	0.13 d	1187.5 ab	0.14 ab	0.92 a
Bronze Rocket	183.0 a	24.9 d	53.6 cd	19.2 b	0.14 cd	950.9 d	0.15 a	0.98 a
White Rocket	182.4 a	29.1 cd	69.8 a	25.1 a	0.20 b	1017.0 cd	0.13 ab	0.57 b
S.E.	3.574	1.921	2.262	1.808	1.45×10^{-2}	51.06	6.95×10^{-3}	4.12×10^{-2}

* The order of the varieties is in accordance with their flowering time, namely the earliest to flower first and the latest last.

** Values in the same column not followed by the same letter are significantly different at the 5% probability level.

density of flower spike, total height, length of flower spike/total height and branching index), all of which are concerned with the quality of the product, the interaction variances were less than 10% of the accumulated value. In all of these, the error variance value was higher than 35%. This indicates that the variability within each variety is higher than might be expected from F1 hybrid cultivars. Three of these characters, - density of flower spike, length of flower spike/total height and branching index have genotypic variance values of about forty percent or more. Since the genetic variability is relatively high it may be possible to select for better quality for these characters.

The effect of environment was comparatively high for two of the characters examined - time from budding to flowering, and leaf number. These characters, together with budding time, also had the highest values for genotype-environment interaction. The growth period of each genotype examined therefore was mainly dependent on environmental conditions.

Computations were made to determine the heterogeneity of the regression values and the magnitude of the residual sum of squares, the latter indicating the deviation of the actual measurements from the linear regression line of each variety over the 27 calculated environmental means. The results of these analyses are also given in Table 1.

The proportion of the interaction sums of squares which can be accounted for by linear regression was also calculated for each character, using the method

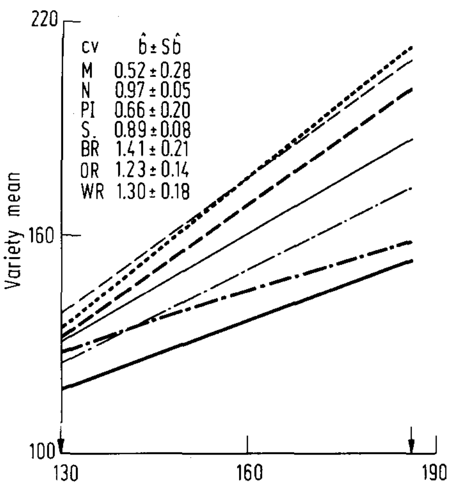

Fig.1

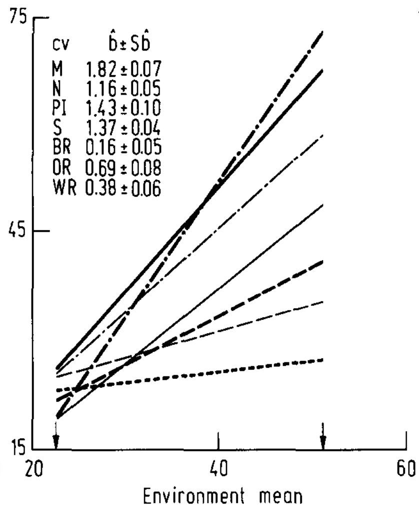

Fig.2

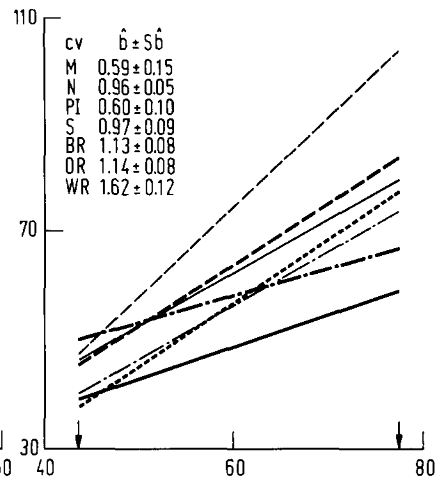

Fig.3

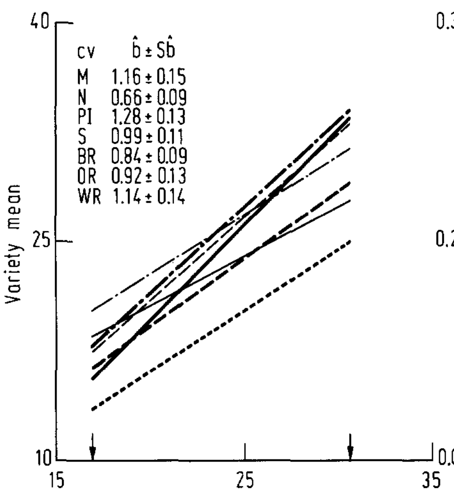

Fig.4

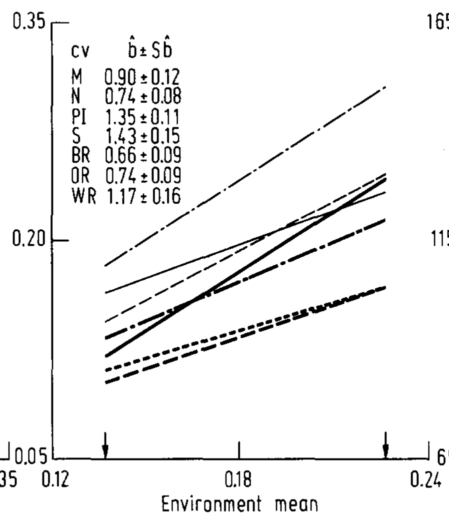

Fig.5

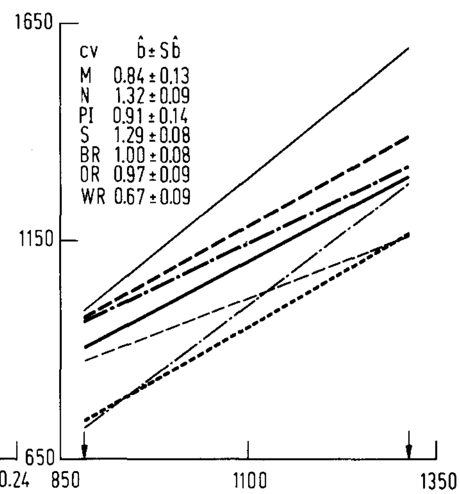

Fig.6

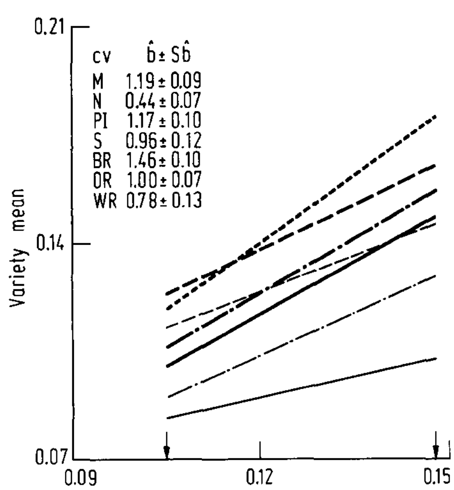

Fig.7

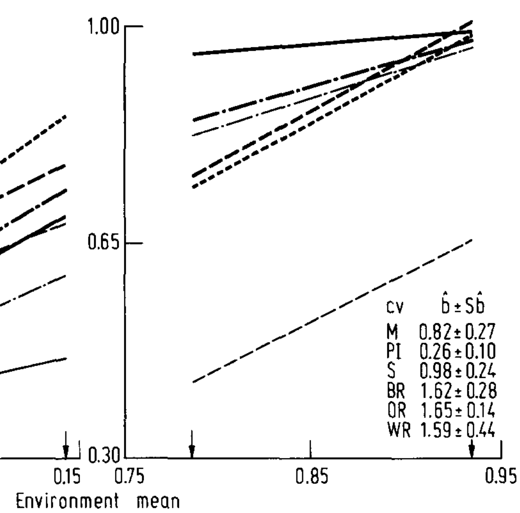

Fig.8

of Fripp and Caten (1971). The high values obtained clearly indicate that most of the genotype-environment variance could be explained by differences between the slopes of the regression lines. The relatively small residual mean squares, however, are still significantly greater than the error item so that there are deviations from linearity which cannot be explained in terms of experimental error.

The means of the performance of each genotype over the range of environmental regimes are given in Table 3, and the regression graphs with the slope of each regression line in Figs. 1 to 8.

Budding time

This character can be used as a measure of earliness. It can be seen from Fig. 1 that Pink Ice and Montezuma are the most stable varieties as reflected by their low regression coefficient values ($\hat{b}$), and that over all the tested environmental conditions these cultivars took the lowest number of days to produce the first recognisable macroscopic flower bud. Usually the order of earliness (Table 3) corresponds with the order of stability as measured by the $\hat{b}$ values (Fig. 1); therefore the longer the growth period before the flower bud develops the more sensitive the varieties are to worse or better conditions.

Time from budding to flowering

The period of development from the bud stage to the anthesis of the first flower also plays an important role in the determination of earliness or lateness of a cultivar.

The extreme differences in the degree of varietal response for this character were reflected by the slopes of the regression lines (Fig. 2). The variety which had the most uniform response to environment was Bronze Rocket ($\hat{b} = 0.16 \pm 0.05$), while Montezuma, was the most sensitive variety to environment and had a much steeper regression line ($\hat{b} = 1.82 \pm 0.07$).

The mean time required from budding to flowering also showed extreme variation between cultivars, from twenty five to forty one days in Bronze Rocket and Pink Ice, respectively (Table 3). The highly significant negative correlation ($r = -0.980$, $P < 0.1\%$) between budding time and time from budding to flowering suggests that the two processes are correlated. If such a correlation could be broken, the possibility would exist for the development of an early variety which combines the fast vegetative growth and low sensitivity to environment changes during this phase of the early varieties, with the rapid spike development of the latter summer flowering types (see Rabinowitch *et al.* in press).

Leaf number

This character can be used as another determinant of earliness (Hedley 1974; Arthur and Hedley in press). The early varieties, Pink Ice and Montezuma were the most stable cultivars (Fig. 3), with relatively small changes in leaf number occuring with changes in environment. The late cultivar, White Rocket was the most sensitive to changes in environmental conditions. On average, Pink Ice had the smallest and White Rocket the largest leaf number over the 27 different environmental conditions (Table 3).

A variety such as Pink Ice, with the lowest leaf number and the lowest number of days to budding would be most desirable in a breeding programme where earliness and the stability of such a character is required.

Number of flowers per spike and spike density

For a cut flower such as *Antirrhinum* the number of flowers on a spike is of prime economic importance. It seems from our experimental results (Table 3) that over the range of environmental conditions, all the commercial varieties had on average sufficient numbers of buds and flowers on their spikes to be commercially acceptable. Significant differences between cultivars do exist however, and over all environmental conditions Bronze Rocket had fewer flowers per spike as compared to Montezuma, Snowman and White Rocket (Table 3). There are also great differences in the degree of response of production of flowers in regard to changes in environment (Fig. 4). Hence, Navajo was far more stable ($\hat{b} = 0.66 \pm 0.09$) than Pink Ice ($\hat{b} = 1.28 \pm 0.13$) over the range of environments used.

The number of flowers per spike is not the only criterion determining the quality of the cut flower, - the number of flowers per unit length of the spike is also of paramount importance. A great variation in flower density was found between varieties (Table 3), ranging from Snowman, with flowers at 4 mm intervals over all environments, to Orchid Rocket and Bronze Rocket which had flowers at twice that distance apart. Large differences in sensitivity to environment were also found for this character (Fig.5). The most unstable cultivar was Snowman which responded markedly to improving environment as measured by environmental means.

All the cultivars tested therefore will produce on average enough flowers per spike, but the differences in the density of the flowers among the varieties and the big variation in the degree of response of these two characters, makes a more stable variety like Navajo a suitable source of genetic variability for spike quality.

Total height and length of spike/total height

Another important character associated with the quality and saleability of a cut flower is the total height of the product, a taller plant being preferred to a shorter one.

On average most of the cultivars tested achieved acceptable values for total height (Table 3). With the exception of White Rocket all of the varieties showed average or above average responses to changes in the environment and therefore would tend to give low quality flowers under poor conditions (Fig.6).

A highly important character related to total height is the relationship between the length of the spike and the length of the stem; tall plants with a high ratio of spike to stem are desirable. Under very poor conditions, when the plant is likely to be short, a good combination of these two features becomes more difficult to achieve. The tested cultivars have shown considerable variation in this respect, ranging from Navajo with spikes that were less than 10 % of the total height, up to 15 % for Bronze Rocket (Table 3).

There were also large differences in sensitivity to changes in the environmental conditions (Fig.7). Navajo was apparently the most stable ($\hat{b} = 0.44 \pm 0.07$) but it also had the worst performance, while Bronze Rocket was highly sensitive to environmental conditions ($\hat{b} = 1.46 \pm 0.10$).

A combination of tall plants with relatively high values for the ratio of length of spike/total height of about 13 % and relatively low sensitivity to changes in environment can be found in White Rocket ($\hat{b} = 0.78 \pm 0.13$).

Branching index

This character is of great economic importance since prior to sale as a cut flower there is a requirement for long branches to be removed.

It is clear (see Table 2) that over fifty percent of the accumulated variance values for this character can be accounted for by the differences between varieties (σ^2VAR) and an additional thirty-six percent can be attributed to differences within genotypes (σ^2E). It should be possible therefore to select plants with small branches. Although White Rocket was very sensitive to environmental changes (Fig.8), this variety nevertheless gave the lowest "Branching index" mean value over all environmental conditions (Table 3). While Pink Ice was the most stable variety (Fig.8) it also had the highest mean value for this character (Table 3). The regression line for Navajo is not presented, as the regression mean square in the analysis of variance proved to be nonsignificant.

Conclusions

The experiment described was designed to measure some of the genotype-environment interactions in Antirrhinums. The main emphasis has been laid on economically important characters in relation to horticultural management and to the quality of the cut flower.

The mean square values for all characters examined were statistically significant for the interaction between genotype and environment, for the heterogeneity of regression and for the residual items (Table 1). For these characters, therefore, predictions of varietal responses to environment (Samuel *et al.* 1970) cannot be made reliably. In all cases, however, a high proportion of the interaction sum of squares could be accounted for by linear regression (Table 1). This indicates that linear responses to environment could be demonstrated for all the characters investigated (Figs.1-8) and that the greater part of the genotype-environment interaction could be attributed to the differences between the slopes of the regression lines. It is interesting to notice the differences between early and late cultivars as far as horticultural characters are concerned (Figs. 1-3, 8). For budding time and leaf number, the early forcing varieties were less sensitive to changes in growth conditions, as shown by their lower regression coefficients ($\hat{b}$). This was also true with regard to branching index, except for Navajo which did not respond linearly to environment as indicated by its nonsignificant regression mean square. The picture is reversed, when the time from budding to flowering is considered. Here, the late flowering cultivars had much lower $\hat{b}$ values compared to the early varieties.

The demonstration of large differences between varieties in the expression of their genetic potential under various environmental conditions is of interest, both to the grower and the plant breeder. From the grower's point of view, these results could provide a better background for making decisions regarding the type of variety to use and the kind of response that might be expected. For example, a cultivar such as Bronze Rocket, which had a high mean value for the ratio of spike length to total height (Table 3) was also the most sensitive to environmental changes ($\hat{b}$ = 1.46 ± 1.10, Fig. 7). This variety therefore might produce flowers of low grade quality under suboptimal conditions. On the other hand, it is likely that a variety which is highly responsive to changes in environment will be chosen when better growing conditions are available.

The information presented in this paper could also benefit the plant breeder in exploiting genetic variability for the production of better varieties which have a known sensitivity to environmental changes. The differences in mean values over ranges of environment (Table 3) indicate the level of the average phenotypic expression of the measured characters. The variation in the degree of response between varieties (Figs. 1-8) and the information gathered from the partitioning of the variation (Table 2) could point out available genetical sources for the production of improved *Antirrhinum* varieties.

The mean values of the number of days to budding could aid the breeder in the selection of early flowering cultivars. In this experiment, the varieties ranged from 140 to 182 days (Table 3) with $\hat{b}$ values of 0.66 ± 0.20 to 1.30 ± 0.18 (Fig. 1) for Pink Ice and White Rocket respectively. A relatively high proportion of the variation for this character could be attributed to differences between varieties (Table 2) indicating that selection for early stable types is plausible.

The quality of the cut flower is the result of several plant characters, many of which can be improved by breeding. One of these characters is spike density. The mean values for this character ranged from 0.20 to 0.13 (Table 3) for Navajo and Orchid Rocket respectively, both varieties having a similar low $\hat{b}$ value (Fig. 5). The genetic variation for spike density was about 40 % (Table 2) which again indicates that selection for improved quality is possible. There are cases however where better performance and sensitivity to environmental changes occur simultaneously. For example, Bronze Rocket has the highest mean value for length of flower spike/total height (0.15, Table 3) and is also the most sensitive to environment ($\hat{b}$ = 1.46 ± 0.10, Fig. 7). On the other hand, Navajo which has a relatively low sensitivity to environment ($\hat{b}$ = 0.44 ± 0.07, Fig. 7) also has the lowest mean value (0.09, Table 3). Whether or not a better ratio between spike and stem is tightly correlated with high sensitivity to environment, is yet to be investigated by testing a larger number of varieties. If such a connection exists, the breeder is faced with the alternative of either producing varieties with high quality under specific environmental conditions or less sensitive cultivars which forsake some degree of quality.

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Literature

Arthur, A.E.; Hedley, C.L.: Biometrical analysis of the effect of nitrogen of five varieties of *Antirrhinum majus*. Ann. Bot. (in press)

Edwards, K.J.R.: Effects of temperature on genetic differences in flowering time in *Antirrhinum majus*. Eucarpia meeting on ornamentals, John Innes Institute, Norwich, 1-3 April, pp. 32-40 (1974)

Finlay, K.W.; Wilkinson, G.N.: The analysis of adaptation in a plant breeding programme. Aust. J. Agric. Res. 14, 742-754 (1963)

Fripp, Y.J.; Caten, C.E.: Genotype-environmental interactions in *Schizophyllum commune*. Heredity 27, 393-407 (1971)

Hedley, C.L.: The use of naturally occurring variants in the analysis of flowering of *Antirrhinum majus* L. Eucarpia meeting on ornamentals, John Innes Institute, Norwich, 1-3 April, pp. 41-58 (1974a)
Hedley, C.L.: Response to light intensity and day-length of two contrasting flower varieties of *Antirrhinum majus* L. J. Hort. Sci. 49, 105-112 (1974b)
Hedley, C.L.; Harvey, D.M.: The involvement of CO_2 uptake in the flowering behaviour of two varieties of *Antirrhinum majus*. In: Marcell, R. (ed.), Environmental and Biological Control of Photosynthesis, pp. 149-159. The Hague: Junk 1975
Rabinowitch, H.D.; Hedley, C.L.; Arthur, A.E.: Variation in budding and flowering time of commercial cultivars of *Antirrhinum majus*. Scientia Hort. (in press)
Samuel, C.J.A.; Hill, J.; Breeze, E.L.; Davies, A.: Assessing and predicting environmental response in *Lolium perenne*. J. Agric. Sci. Camb. 75, 1-9 (1970)
Snoad, B.; Arthur, A.E.: Genotype-environment interaction in peas. Theor. Appl. Genet. 44, 222-231 (1974)
Snoad, B.; Arthur, A.E.: The use of regression techniques for predicting the response of peas to environment. Theor. Appl. Genet. 47, 9-19 (1976)

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