

Genotype-Environment Interactions in Peas

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Summary. The experiments described in this paper were designed to measure some of the genotype-environment interactions in peas and the emphasis has been upon the characters which are of importance in relation to the time of maturity, uniformity of maturity and to yield.

Six pea varieties were grown at four sites in Eastern England, there being an early and a late sowing at each site. The data were analysed by means of regression techniques and by the analysis of variance. Linear responses to environment were demonstrated for all the characters in the majority of varieties and the relative importance of some of the components of yield in different environments were determined. The variation could be partitioned into its genetic, environmental and interacting components and genotype-environment interactions were demonstrated for every one of the characters investigated.

Introduction

During the last ten years an increasing amount of attention has been paid to the nature of genotype-environment interactions and to the techniques used for analysing such interactions. These analytical methods have been primarily based upon the demonstration that genotype performance bears a linear relationship to a measure of the environment provided by the mean performance of a number of genotypes (Finlay and Wilkinson 1963).

In a crop such as the pea where the majority of the harvest each year is mechanically vined and processed at a rigidly determined stage of development it is very important that varieties should be as predictable in their performance and as stable in response to environmental influence as possible. Experience has shown that many modern pea varieties do not meet these requirements although the components of the environment which cause this instability are not necessarily known. It is established, however, that peas are particularly sensitive to bad soil conditions such as poor aeration or waterlogging and peat soils lead to excessive growth of haulm and poor pod formation (Anon 1969).

The experiments detailed in this report are designed to measure some of the genotype-environment interactions in peas and the emphasis has been upon characters which are of importance in relation to time of maturity, uniformity of maturity and to yield.

Materials and Methods

Six commonly grown pea varieties representing a range of maturity types, flower numbers and ovule numbers were chosen for these experiments:

1. Dark Skinned Perfection (DSP)
2. Greenshaft, a multi-seeded variety
3. Jade
4. Puget, a multi-podded variety
5. Scout
6. Sprite.

These six varieties were grown at four sites in three widely separated areas in the Eastern half of England with two sowings, one early and the other late, at each. The nomenclature adopted was as follows:

Bedford — site 1	} 1.1 = site 1, sowing 1 1.2 = site 1, sowing 2, etc.
Peterborough — site 2	
Stanfield (peat) — site 3	
Stanfield (sand) — site 4	

The Bedford site, principally a clay, loam mixture was kindly provided by the Unilever Research Station at Colworth House which is about 6 miles N.W. of Bedford and we are greatly indebted to Dr. P. Kyle for providing the original seed as well as the growing, recording and harvesting facilities for these experiments.

The Peterborough site, principally a limestone one was provided by the Pea Growing Research Organisation at Wansford about 8 miles W. of Peterborough and we are pleased to acknowledge all the help and assistance provided there by Mr. G. P. Gent.

The two remaining sites were at the John Innes field station at Stanfield which is about 20 miles N.W. of Norwich. One, as the names imply, being on a high moisture content, alkaline peat and the other a dry, sand and gravel mixture.

Four replicates of each variety were sown in randomised plots using an Oyjord drill at each of the sites. Each plot was trimmed to a final length of 27 ft, there being 3 ft between the plots in each direction. The plots were 4½ ft wide, there being 10 rows in each with six inches between each row. The seed was sown with a target density of ten plants per square foot after allowing for germination and vigour test results (Table 1). Agronomically, each site was treated according to its individual requirements as regards fertilizer treatments etc. Pre-

Table 1. Germination and vigour test results

Variety	Germination (%)	Vigour (µmho)	1000 seed weight (gm)	Weight sown per plot (gm)
Scout	93	17	206.8	333.5
Sprite	95	21	269.6	425.7
Jade	91	34	263.6	434.5
Puget	81	26	203.8	377.4
DSP	96	20	255.2	398.8
Greenshaft	94	25	191.6	305.7

and post-emergence herbicides (Gesagard 50 and Dinoseb acetate) were used on all sites except the Stanfield peat and Gusathion MS was used, if necessary, to control insect pests. The first sowing was made on 21st March and the second on 8th May, 1972.

The achieved plant density of each replicate was recorded when the seedlings were well established and records of the date and accumulated heat unit levels to full flowering for each plot were also noted. (At Peterborough, site 2, flowering time was only recorded for one replicate of each variety.)

The final individual plant measurements were made on 25 plants pulled from a diagonal line in each replicate when the plants had reached the stage at which they would be suitable for canning.

These measurements were:

Node of first pod — including scale nodes
 Number of pods at flowering nodes 1—4
 Number of seeds at flowering nodes 1—4
 Total length of internodes between 1st and 4th flowering nodes.

From these data it was also possible to estimate the number of seeds per pod at nodes 1 to 4 and some idea of yield (the average vining pea contributing 3.8 nodes per plant) by summing the total seed number for nodes 1 to 4.

Analysis of Variance

The factors in these experiments have been considered as random effects and so a random model situation has been assumed and the data analysed were based on the mean of each set of four replicates. In the F tests for the main effects the error term used was the highest, significant interaction mean square. When the interaction mean squares indicated non-significance then the main effects were tested against the error term which had previously been used to test the significance of the interactions. The error term itself, which had 144 degrees of freedom, was derived from the total sums of squares of the means of the four replicates of each variety at each site and each sowing. This error term was chosen because during the early stages of the analysis it became obvious that there were significant differences between replicates for a number of characters and at a number of sites. Consequently, because replicates were combined for analysis, this error term would take into account some of these replicate differences.

The influence of environment, i.e. site or sowing time, is immediately apparent for most characters either as a main effect or as an interaction. Most environmental components are unlikely to be under agronomic control and so will have to be tolerated. Equally there are very significant genetic components again as both main effects and interactions, but these are to some extent in the hands of the plant breeder. The relative proportions of these environmental and genetic components vary from one character to another as can be seen in Table 2.

The magnitude of the genotype-environment interactions ($S_i \times V$: $S_o \times V$: $S_i \times S_o \times V$) relative to the genetic effects is also observable in Table 2.

Again it depends upon which character is being discussed as to the importance of genotype-environment interactions in relation to the main genetic effects.

Regression Analysis

Regression techniques are available which permit genotype-environment interactions to be expressed as linear functions of the environment. In these regressions the environment is measured by estimating the mean performance of a number of genotypes in each of the environments. Thus in the present experiment the behaviour of each variety in an environment is regressed upon the mean value for the six varieties in that same environment and the straight-forward regression technique based upon the original Finlay and Wilkinson methods has been followed; in much the same way as it has been used for analysing herbage grass data (Breese 1969).

Such a regression analysis can be related to the analyses of variance data in Table 2. It is therefore possible to determine for each character how much of the genotype-environment interaction can be accounted for by the heterogeneity of the regressions, that is by the differences between the slopes of the regression lines, and how much is residual and therefore unpredictable. The results of this partitioning of the genotype-environment interaction terms are also summarised in Table 2, the two components each having been tested against the error term derived for the analysis of variance. Regardless of which character is being examined a significant part of the genotype-environment interaction can always be demonstrated as being due to the differences between the slopes of the regression lines. In the majority of instances too the unpredictable or residual deviations are also significant.

Table 2 will not provide much further information and it is necessary to consider the individual regressions now in some detail in order to begin their interpretation.

First of all it is important to note the relationships of the regression lines, that is whether or not the ranking order of the genotypes remains unaltered over the whole range of environments under test. When a differential response is demonstrated but the ranking order of two genotypes remains unaltered there is a clear indication of the optimum environment for such genotypes. If, however, a reversal of ranking order is demonstrated then each genotype might perform better in specific, and possibly widely contrasting, environments. This type of information is of great value because should the environment be partly under control by for example alteration in sowing time, density of plants, fertilizer treatment and so on then it may be possible to provide the appropriate environment for selected genotypes. There are also indications of which genotypes are likely to be of most value in each of the environ-

Table 2. *Degrees of freedom and mean squares derived in the analyses of variance of the data*
(* = 5.0-1.0% : ** = 1.0-0.5% : *** = <0.5%)

	d.f.	Days to† flower	AHUs to† flower	Node of first pod	Dist. bet. 1st & 4th fl. node	Pods at Node 1	Pods at Node 2	Pods at Node 3	Pods at Node 4
Sites (Si)	3	40.32***	27578.81	1.60	451.18*	1.00	0.77	1.09	1.04
Sowings (So)	1	8053.61***	8138.02	0.47	729.67*	0.00	0.21	0.71	2.78
Varieties (V)	5	238.52***	13997.10***	30.91***	160.54***	0.20	0.27***	0.09	0.14***
Si × So	3	7.71	5781.04***	0.28***	26.25***	0.15**	0.09*	0.15*	0.29***
Si × V	15	1.60	159.03	0.09*	5.15*	0.13***	0.05	0.05	0.02
So × V	5	6.06	53.36	0.12*	9.59*	0.07	0.06	0.01	0.06
Si × So × V	15	2.90***	194.33***	0.07	2.13*	0.02*	0.02*	0.04***	0.02*
Heterogeneity of regression	5	11.89***	178.93***	0.15*	6.28***	0.25***	0.05***	0.11***	0.10***
Residual	30	1.27***	155.76***	0.08*	4.19***	0.05***	0.04***	0.03***	0.02***
Error	144	0.11	11.32	0.05	1.26	0.01	0.01	0.01	0.01

	d.f.	Seeds per pod at node 1	Seeds per pod at node 2	Seeds per pod at node 3	Seeds per pod at node 4	Seeds at node 1	Seeds at node 2	Seeds at node 3	Seeds at node 4	Total seeds at nodes 1-4
Sites (Si)	3	27.22*	20.47***	9.27***	3.26*	50.77	37.54	15.82	3.53*	385.91*
Sowings (So)	1	9.17	4.95	0.95	0.23	9.57	1.97	0.85	3.34	2.36
Varieties (V)	5	6.55**	5.96***	4.11*	4.00***	15.72*	13.67***	7.21*	4.30***	57.33
Si × So	3	2.16***	0.89*	0.12	0.39	7.59***	4.16**	2.08*	0.31	34.04***
Si × V	15	1.33***	0.95***	0.95***	1.10	4.15***	1.93*	1.59**	1.43	20.06***
So × V	5	0.19	0.10	0.35*	0.53	0.36	1.03	1.27*	1.31	3.90
Si × So × V	15	0.25	0.23*	0.17	0.71***	0.87***	0.74***	0.44***	0.77*	6.18
Heterogeneity of regression	5	2.03***	1.99***	1.08***	1.04***	5.55***	2.19***	2.02***	2.11***	14.33***
Residual	30	0.49***	0.28***	0.44***	0.82***	1.64***	1.14***	0.89***	0.96***	11.38***
Error	144	0.16	0.12	0.12	0.26	0.16	0.12	0.12	0.44	4.01

† error term has 108 d.f. (Only one replicate of each variety scored at site 2).

ments used in the experiments. As can be seen in the subsequent regressions (Figs. 1 to 7) both types of situation, with and without changes in ranking order, have been revealed. For the purpose of this paper it has been decided to adopt as simple an approach as possible and to confine the comments on the data to the *degree* of response only. The six regression lines allow comparison of each variety with the average of the six. This means that regressions of unit slope have an average degree of response, those in excess of unity an above average degree of response and vice versa. Generally speaking, the plant breeder will be interested principally in varieties with below average response which have at the same time high levels of, say, yield. However there may be instances when a high yield over a small range of environments will be preferable to a below average response to a wide range of environments when it happens to be coupled with a lower yield. So much will also depend upon whether it is possible to control the environments.

A total of 17 characters is available for analysis from these experiments and it is proposed to take these in sequence.

Results and Discussion

Time of First Flower

This is a character which is of practical importance since it is used in the prediction of harvest dates. The

system of genetic control is a simple, additive, polygenic one (Snoad and Arthur, 1973a). However speed of development in peas can be better correlated with some measure of energy input than with time. Accumulated Heat Units (AHUs) are used for this purpose and they are derived from the running total of the amount by which the mean daily air temperature exceeds 4.5 °C. Consequently, flowering time has been analysed in relation to days and also to AHUs.

Extreme differences between the two forms of measurement are immediately apparent from the analysis of variance (Table 2). Using time as a factor the main effects of site, sowing and variety are significant with sowing time being of greatest importance and genotype-environment interactions confined to sites × sowings × varieties. Using AHUs for reference, however, the interpretation is different and the only significant main effect is varietal but the genotype-environment interaction component is the same as for days to flower.

Despite these differences in the analysis of variance the regressions which are obtained are remarkably similar (Fig. 1). All the varieties exhibit an average response to the environments and the ranking tends to be similar in both sets of regressions. There is, however, a significant difference between the ranking of the environments in that sowings 1 and 2 are clearly separated in the day regression but integrated in the AHU regression. This indicates how much

more efficient it is to use AHU data rather than time and this can be clearly demonstrated by splitting up the regressions into sowing 1 and sowing 2 (Fig. 2). In accordance with expectations there is a greater similarity between the first and second sowing data using AHUs than when using days. In addition the first and second sowing AHU regression results are closer to the combined AHU regression data. Two varieties, Sprite and Scout did exhibit respectively a below and an above average response to environment in the second sowing although the variance ratio for Sprite is too small for the regression to be interpreted as more than a trend.

Stanfield sites, both peat and sand, tended to produce earlier peas — as measured by AHUs — than Peterborough and Bedford.

The Node of the First Pod

This character is often a useful guide to the earliness of a pea plant and in most cultivars there is a very high correlation between the node of the first flower and the time of flowering. However, this does not always obtain (Snoad and Arthur 1973b) and it certainly is not true in this present series of experiments (Table 3). The very low correlation demonstrated here is probably due to the difference between rates of development in sowings 1 and 2 and a high correlation can be shown to exist only if it is attempted *within* sowings. A high correlation can be demonstrated between AHUs to first flower and the node of the first pod even *across* sowings (Table 3). It must be remembered, however, that these correlations are slightly different because it is the node of the first pod and not the first flower that is used and there could well be an abortion factor involved which has not been taken into account in these ex-

Table 3. Correlations between days or AHUs and node of first pod (* = 5.0–1.0% : ** = 1.0–0.5% : *** = <0.5%)

Over varieties sites and sowings	Days	AHUs
	0.2918*	0.6107***
Over varieties and sowings,		
site 1	0.2912	0.9395***
site 2	0.2908	0.9051***
site 3	0.2002	0.8337***
site 4	0.3484	0.7164***
Over varieties		
site 1		
sowing 1	0.9773***	0.9763***
sowing 2	0.9869***	0.9880***
site 2		
sowing 1	0.9369**	0.9006*
sowing 2	0.5462	0.9194**
site 3		
sowing 1	0.9977***	0.9859***
sowing 2	0.9456**	0.9314**
site 4		
sowing 1	0.9775***	0.9779***
sowing 2	0.9425**	0.9310**

periments. The analysis of variance (Table 2) shows the main differences to be varietal but there are significant genotype-environment interactions involving this character too and the difference between the regressions does account for part of this interaction.

The regressions obtained using these data show that only one variety, Puget, exhibits an average response to environment (Fig. 3). Regressions could not be obtained for Greenshaft and Jade since the variance ratios were non significant but the remainder show somewhat above and below average responses.

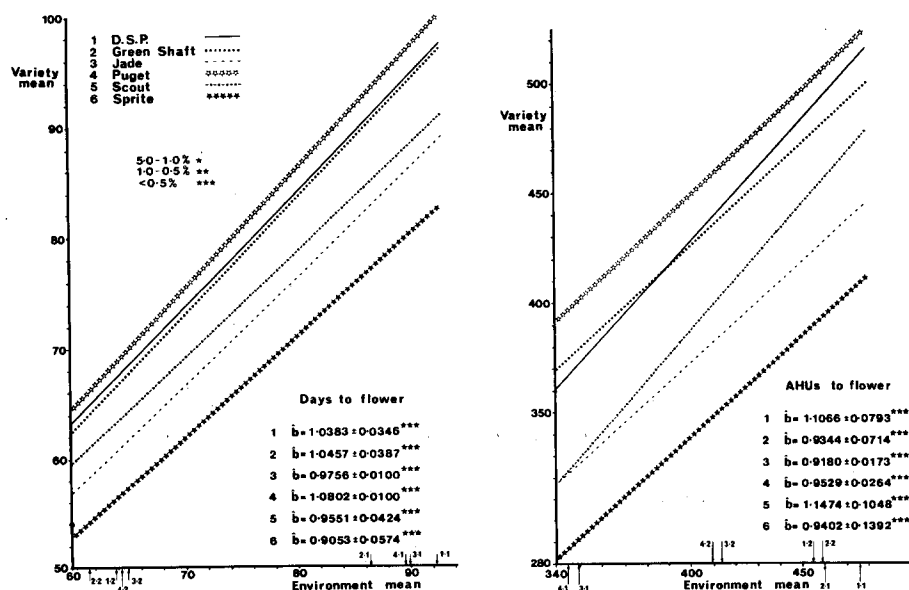


Fig. 1. Regressions for flowering time using days or AHUs

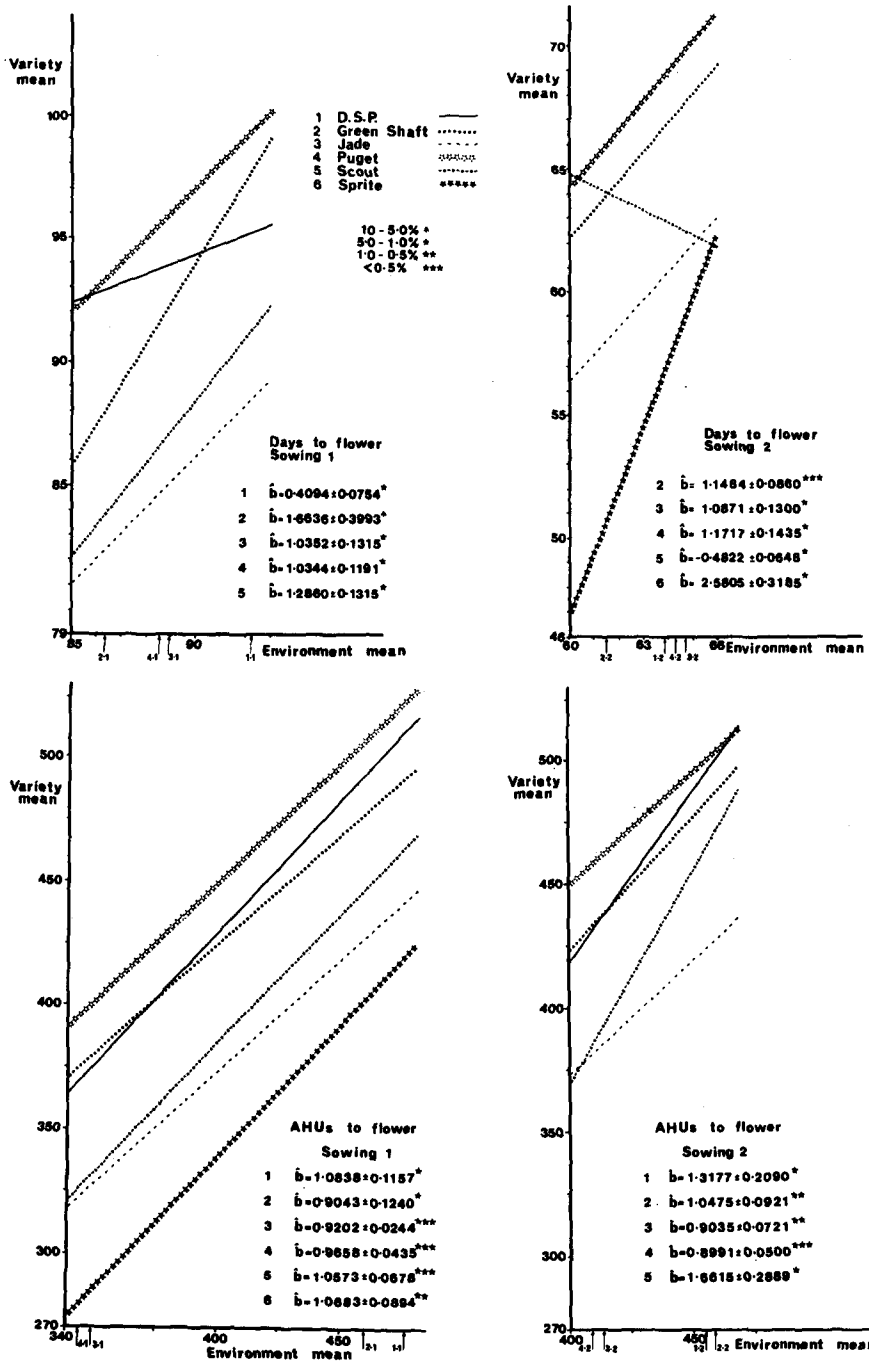


Fig. 2. Regressions for flowering time using days or AHUs with partitioning into sowing 1 and sowing 2

Even these regressions have rather high standard deviations which introduces some uncertainties into interpretation. This is an unexpected finding since previous genetical studies, using sets of diallel crosses, have indicated that the closely associated character node of first flower is a reliable one and under a simple, additive system of genetic control (Rowlands 1964, Snoad and Arthur 1973a and b). Again there is a possible abortion factor which has to be

considered as responsible for the comparatively poor regressions obtained using this node of first pod data.

Distance between the First and Fourth Flowering Node

Because about four successive nodes from each individual vining pea plant will contribute to the yield it is of value to measure the distance up the stem from the first to the fourth fruiting node. It is quite conceivable that the shorter this distance

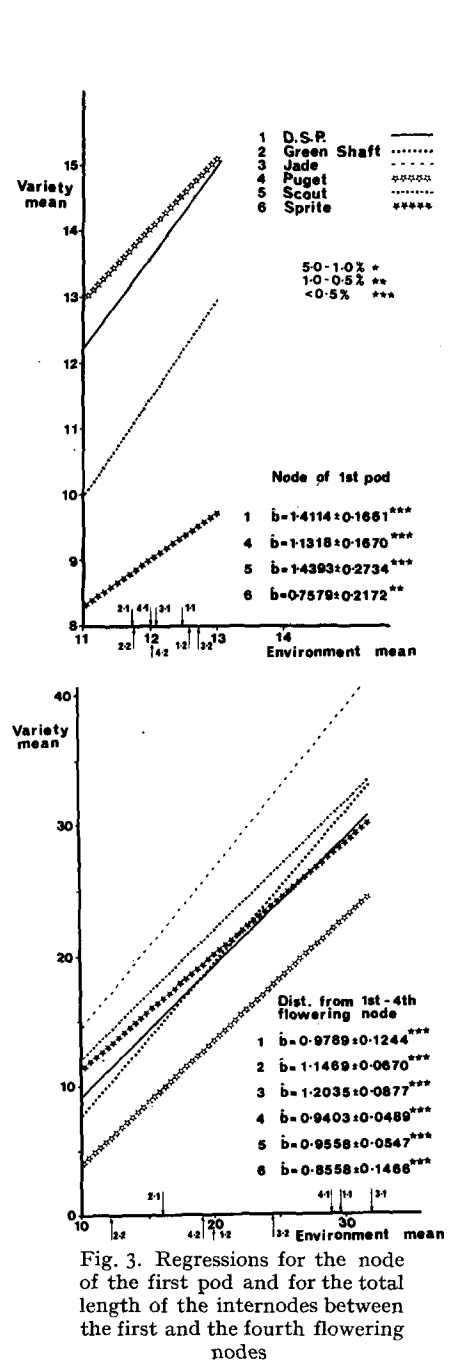


Fig. 3. Regressions for the node of the first pod and for the total length of the internodes between the first and the fourth flowering nodes

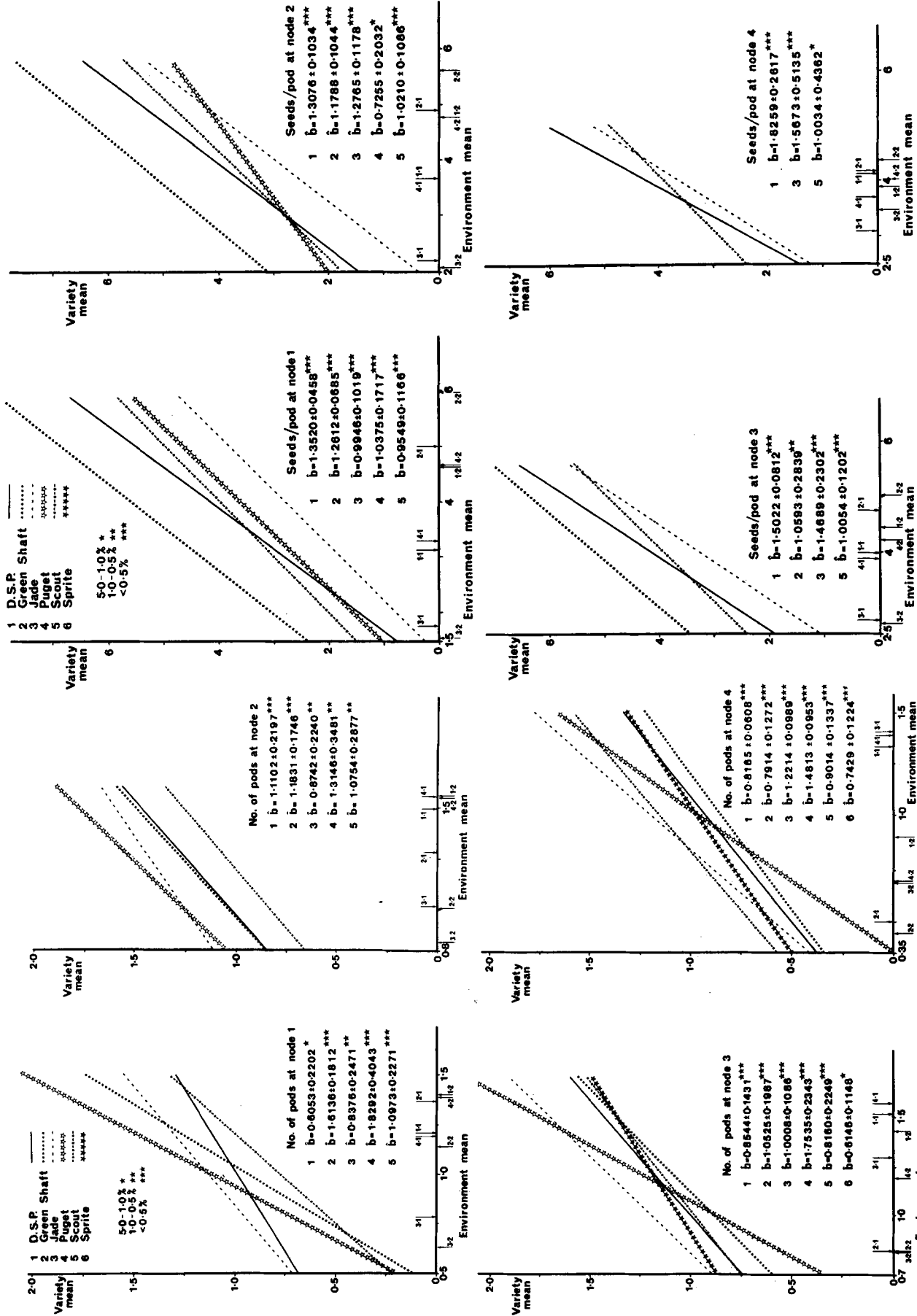


Fig. 4. Regressions for the number of pods at each of the first four flowering nodes

Fig. 5. Regressions for the number of seeds per pod at each of the first four flowering nodes

then the smaller the maturity spread might be and to reduce the maturity spread is a commercially desirable objective in peas.

The analysis of variance of these data shows the most significant main effect to be varietal although sites and sowing times are also significant (Table 2). Genotype-environment interactions are also indicated and, once more, differences between the regressions account for a significant proportion of these interactions.

The regressions suggest that most of the varieties have an average response to environment with perhaps Jade being above and Sprite below average (Fig. 3). The environment in which the shortest internodes developed, regardless of sowing time, was at Peterborough. The general tendency is for longer internodes to be developed at the first sowing than the second which could be a function of the amount of light. It is interesting to note that the response to environment is similar in both sowings with the ranking of the environments being identical.

Pods per Node

The analysis of variance of the data from the first four flowering nodes indicates immediately that there are significant differences between the four nodes (Table 2). The majority of the main effects would be significant if tested against the main error term but this significance is lost when the interaction components are used for testing. A significant proportion of the genotype-environment interactions can be accounted for by differences between the slopes of the regression lines and the deviation component is always significant.

The regression analyses demonstrate some of the differences between the four nodes and they also help in differentiating between the behaviour of the six varieties (Fig. 4). The variance ratios increase and the standard deviations decrease indicating better regression lines as one progresses up the plant but the first node would appear to be a very unreliable one to score as being typical of a plant.

The multi-podded variety Puget exhibits the most response to environment at all four nodes and it is also very different from the other five varieties in that it outyields them all but only in "good" environments. For selection and for commercial purposes it is therefore very important to grow this variety and perhaps all multipodded varieties, only in these "better" environments.

Seeds per Pod

This is an important component of yield and Table 2 summarises the analysis of variance results for the number of seeds per pod at fruiting nodes 1 to 4. Site differences are of importance as indeed are varietal differences and genotype-environment interactions are also significant at all four nodes.

The regressions demonstrate the generally high-yielding capability of the multiseeded Greenshaft over most environments (Fig. 5). As with the number of pods per node there are differences between the nodes in terms of degree of response of some of the varieties. The variance ratios for Sprite were always and for Puget sometimes too small to permit regressions to be performed and so only trends can be observed for these varieties. The number of seeds per pod for Sprite when grown in Peterborough was always much lower than might have been expected and this discrepancy is responsible for the high standard deviations and low variance ratios encountered at all four nodes. The omission of this site data results in the establishment of as good a linear relationship for Sprite as has already been established for the remaining five varieties in Fig. 5. At the fourth node, only DSP, Scout and Jade data were reliable enough for regression analysis which suggests that stability of response for this character is particularly poor at this node. Accordingly the predictive power of this technique would be very weak for the majority of these varieties at these higher flowering nodes.

Seeds per Node

This character is also a component of yield but it is a compound one in that it takes into account pods per node and seeds per pod. Records were kept of this character at the first four flowering nodes and the analysis of variance results of these data are summarised in Table 2.

The most significant main effects are varietal and only at the fourth node did the site appear to have any influence upon the number of seeds. Genotype-environment interactions are highly significant and the differences between the regressions appear to account for much of this interaction at all four nodes.

The regressions emphasise the superiority of the variety Greenshaft over all others at the first three fruiting nodes (Fig. 6). In terms of yield these regressions indicate that improvements over at least three nodes and over most sites and sowings is more likely to come from increasing the number of ovules per pod than by increasing the number of flowers per node. A combination of the two characters may prove to be of decided advantage however. Unfortunately the variance ratios for the Sprite regressions at nodes 1 and 2 and for Puget at nodes 3 and 4 were non significant and so they are not depicted although their trends have been noted. Of the remaining varieties, DSP exhibited a uniform and average response to environment at three nodes while Jade and Scout responded more and Greenshaft less from the first node to the fourth node.

Yield of the First Four Nodes

In order to obtain some final assessment of the potential of these six varieties when grown at the

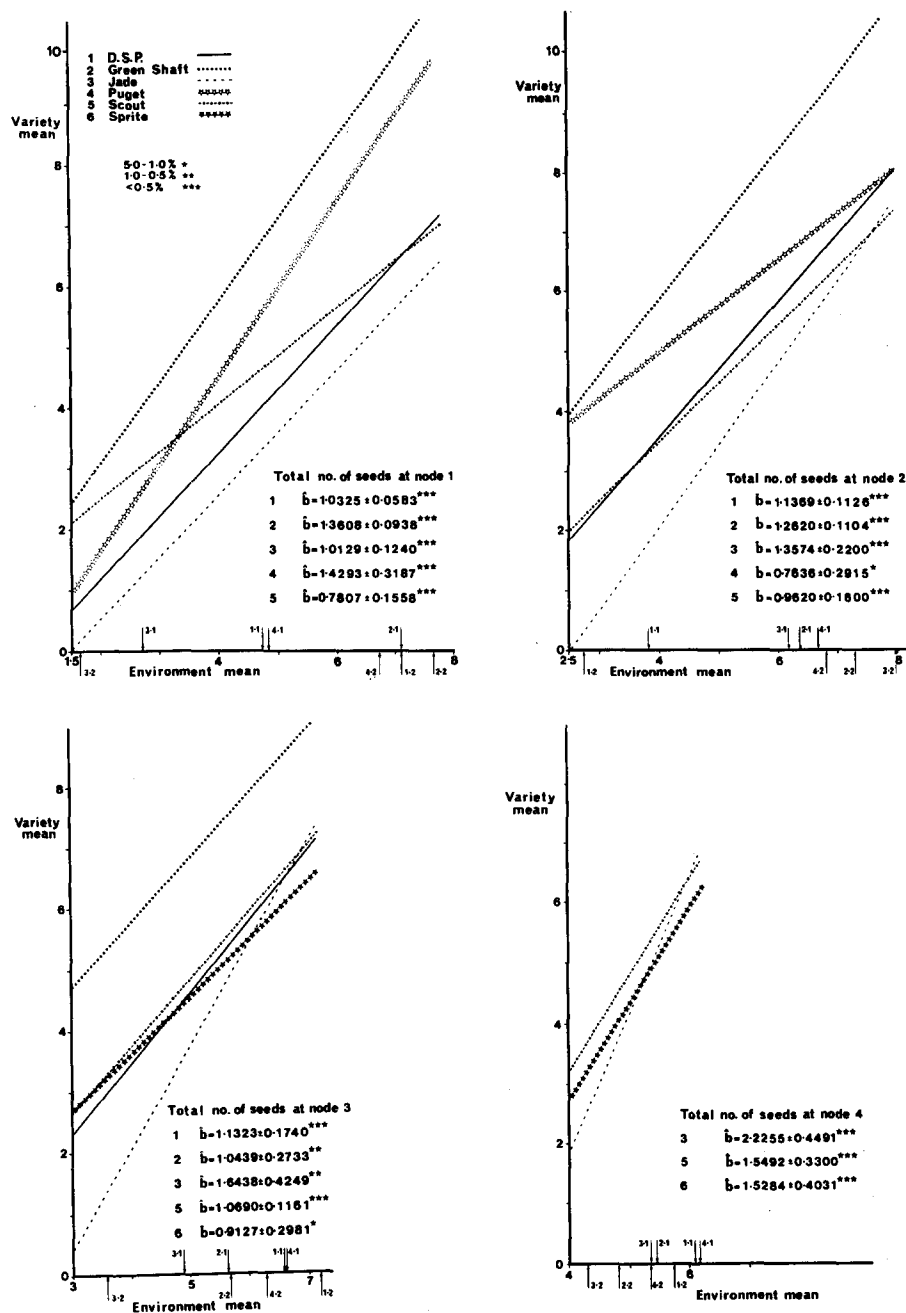


Fig. 6. Regressions for the total number of seeds at each of the first four flowering nodes

four experimental sites the number of seeds per node was summed for the first four nodes. The analysis of variance of these data is given in Table 2, from which it is apparent that of the main effects only sites are of significance. The varieties are significant when tested against the error term but the significance of the genotype-environment interaction components results in the varietal differences being clasped as non significant.

The regression analyses show very clearly the superiority of Greenshaft over the other five varieties (Fig. 7). Puget and Sprite are interesting in that their performance relative to DSP, Scout and Jade

improves in the "poorer" environments which in this set of experiments happen to be the first and second sowings on the high moisture peat. Because yield is multiplicative the regression depicted in Fig. 7 was repeated after having converted all the original data to logarithms. The result is so similar to that obtained using arithmetic data that it would not alter the interpretation in any way.

Conclusion

This is probably the first attempt to exploit the statistical technique developed by Finlay and Wilkinson (1963) for comparing the performance of some

varieties of peas over a number of environments. These experiments encompass a wider range of characters than has generally been analysed in such genotype-environment interaction experiments where the emphasis has usually been upon yield alone. Linear responses to environment could be demonstrated for a large number of characters in the six pea varieties and in combination with an analysis of variance it has been possible successfully to partition the variation into its genetic, environmental and interacting components. Additionally the regressions have provided information on the relative behaviour of the six varieties as well as indications of the relative importance of some of the components of yield in different environments.

The importance of using appropriate units of measurement are emphasised by the flowering time results where using AHUs instead of days makes sense of a nonsense situation. Not only do the regressions from sowing 1 data match those from sowing 2 but also the expected correlation between flowering time and node of first pod can be obtained over both sowings.

Genotype-environment interactions are indicated for every one of the characters investigated. In every instance too a significant part of this interaction could be ascribed to the heterogeneity of the regression lines. The residual component was also significant in every instance and so there is always some unpredictable or unaccountable variation present. Presumably this variation could be due to the micro-environmental influences which are not measurable and so not taken into account in these experiments.

Micro-environmentally influenced differences could have resulted from the slight plant density differences between replicates. The effects of such density variation upon the characters measured are unknown and may be worth pursuing but as such variability is probably encountered under field conditions it is perhaps a factor which has to be tolerated. One way in which replicate differences of this type could be handled would be to treat each replicate as an environment. Such a method is beyond the scope of this present paper but will be considered elsewhere.

The characters with the most uniform and average response to environment in all six varieties are flowering time and internode length. By contrast, the node of the first pod and all the components of yield either differ in response from variety to variety or are apparently non-linear. The fourth node is the most unpredictable of those investigated and frequently provides seed number data which cannot be analysed by regression techniques. With regard to pods per node, however, the fourth node data are as reliable as those from nodes two and three.

One variety in particular, Sprite, seems characteristically to provide data which could not be

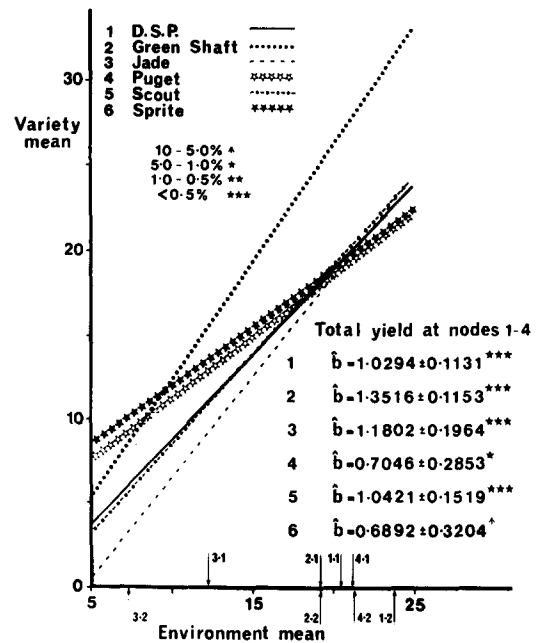


Fig. 7. Regressions for the total number of seeds at the first four flowering nodes

analysed by regression techniques and this applies particularly to yield and its components. This lack of linearity appears to be due to site-specific responses at Peterborough at both sowings but it is not intended to discuss this irregularity further in this paper.

The stress environment, Stanfield peat, could usually be associated with reductions in yield and its components but Peterborough was not an environment particularly conducive to a larger number of pods per node.

The least stable variety for pods per node was undoubtedly Puget, and this particular variety is obviously better suited to good environments only. The multi-seeded variety Greenshaft appeared to outyield all other varieties and, although it frequently exhibited above average responses, it would seem to be a better-yielding proposition than the multi-podded variety Puget.

In general terms the suitability of the analysis of variance and regression techniques for estimating genotype-environment interactions associated with a number of characters in peas has been demonstrated and it remains now to extend these experiments over more years in order to provide more environments. In these subsequent experiments the seed used will all have come from one site and so any variability due to differences in the origin of the seed that might have been experienced in this first experiment will be minimised.

There have been a number of criticisms of these regression techniques and Knight (1970) has been concerned about five main points affecting yield:

1. Sub- and superoptimum mean yields of equal value might be juxtaposed.

2. Different limiting factors can result in equally low mean yields but differences in ranking of genotypes will not be easily recognised.

3. Beyond a threshold level some genotypes may not yield at all.

4. Combining data from different lengths of growing period or from different growth phases can be misleading.

5. The scale of an analysis is important and it cannot be assumed that any one scale will be appropriate for all genotypes in an experiment.

Freeman and Perkins (1971) have criticised the regression technique because the environment is assessed by the mean of the genotypes grown in it. They recommend that the environment should be assessed by the responses of genotypes similar to those under test and grown as standards. This would overcome their original objection that the regressions are statistically invalid because the sum of squares for the joint regression is the same as the total sum of squares between environments and not part of it. Such an approach can be adopted for the *Pisum* data since one or more of the replicates at each site and for each sowing data could be used for estimation of the environment.

There appear to be two definitions of stability in use. Finlay and Wilkinson (1963) use the slope of the regression line as a measure of stability over environments but this is referred to as the degree of response by Breese (1969). According to Breese, stability of response can be estimated from the standard errors of each regression line which measure the scatter of points about each line. In other words, these are the unpredictable irregularities in the response of genotypes to environmental stresses and this definition is the same as that proposed by Eberhart and Russell (1966).

During the analysis of these *Pisum* data we have been aware of these published criticisms of the basic regression technique. This paper has, however, been confined to a simple presentation with the emphasis on the degree of response only. It is intended to use these data for a more detailed investigation of some of the points of criticism in a further publication.

Acknowledgement

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Literature

- Anon: Ministry of Agriculture, Fisheries and Food Bulletin No. 81. London: HMSO 1969.
- Breese, E. L.: The measurement and significance of genotype-environment interactions in grasses. *Heredity* **24**, 27–44 (1969).
- Eberhart, S. A., Russell, W. A.: Stability parameters for comparing varieties. *Crop Sci.* **6**, 36–40 (1966).
- Finlay, K. W., Wilkinson, G. N.: The analysis of adaptation in a plant-breeding programme. *Aust. J. Agric. Res.* **14**, 742–754 (1963).
- Freeman, G. H., Perkins, J. M.: Environmental and genotype-environmental components of variability. VIII. Relations between genotypes grown in different environments and measures of these environments. *Heredity* **27**, 15–23 (1971).
- Knight, R.: The measurement and interpretation of genotype-environment interactions. *Euphytica* **19**, 225–235 (1970).
- Rowlands, D. G.: Genetic control of flowering in *Pisum sativum* L. *Genetica* **35**, 75–94 (1964).
- Snoad, B., Arthur, A. E.: Genetical studies of quantitative characters in peas. 1. A seven-parent diallel cross of cultivars. *Euphytica* **22**, 327–337 (1973a).
- Snoad, B., Arthur, A. E.: Genetical studies of quantitative characters in peas. 2. A six-parent diallel cross of cultivars and primitive forms. *Euphytica* **22**, 510–519 (1973b).

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